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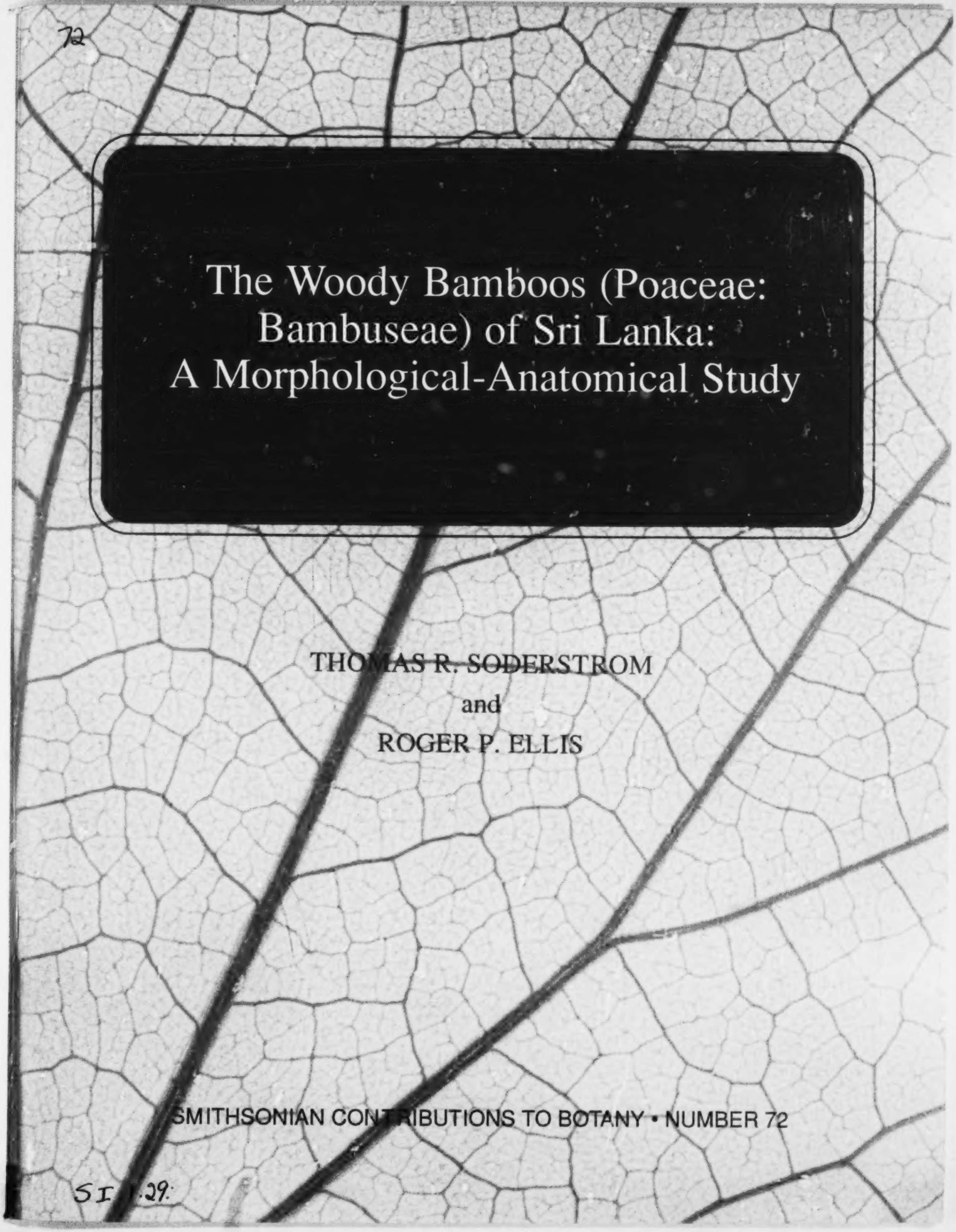

The Woody Bamboos (Poaceae: Bambuseae) of Sri Lanka: A Morphological-Anatomical Study

THOMAS R. SODERSTROM
and
ROGER P. ELLIS

SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 72

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The Woody Bamboos (Poaceae: Bambuseae) of Sri Lanka: A Morphological-Anatomical Study

Thomas R. Soderstrom
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ABSTRACT

Soderstrom, Thomas R., and Roger P. Ellis. The Woody Bamboos (Poaceae: Bambuseae) of Sri Lanka: A Morphological-Anatomical Study. *Smithsonian Contributions to Botany*, number 72, 75 pages, 45 figures, 1988.—Three subtribes of the Bambuseae are present on Sri Lanka, including six genera and 12 species, and they are described both morphologically and anatomically. In the Arundinariinae, five species of fargesioid arundinarias occur: *Arundinaria debilis, A. densifolia, A. floridunda, A. walkeriana*, and the new species *A. scandens;* all are shrubby plants that grow in cool mountain forests and bogs. Three genera of Bambusinae are present. *Bambusa* is represented by three introduced, cultivated species, and *Dendrocalamus* by the new species *D. cinctus*. The new genus *Pseudoxytenanthera* is described, and the single species *P. monadelpha* is unusual in the subtribe in its thin, soft culms produced in open clumps, vine-like habit, and combination of 2–3 stigmas and a branching pattern in which the large central bud remains dormant with the simultaneous production of basal branches, followed by development of the central bud into an elongate whip-like shoot. The Schizostachydinae are represented by *Ochlandra stridula* and *Davidsea attenuata*, the latter a new monotypic segregate of *Teinostachyum* and differing from that genus in its intravaginal branching pattern with three major and several subsidiary branches with the major branches elongating and becoming whip-like, and in its elongate style and plumose stigmas.

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Foreword

The events that led to the publication of this study as part of the Flora of Ceylon Project have been recounted in some detail in a companion piece, a study of the herbaceous bamboos of Sri Lanka (Soderstrom et al., 1987). I will only note here that in the late 1970s, when I approached the collection of Sri Lanka bamboos, I was confronted with a suite of genera in many ways unlike those of the New World with which I was most familiar. Species from Sri Lanka called *Chimonobambusa* and *Indocalamus*, for example, were unlike the Chinese and Indian species assigned to these genera. In order to know where to place the Sri Lanka species I had to learn everything possible about the genera to which they were assigned.

It was necessary to go to the hill country of southern India, to the Himalayas, and to Assam to collect species possibly related to those of Sri Lanka; such a trip I did make during September through November of 1978. A trip to the People's Republic of China in November 1979 was also of great benefit to my understanding of Asian bamboos. Other trips to India, Laos, and South Africa have given me further insights into bamboo relationships. I was also able to briefly visit Madagascar in November 1985, where there are so many endemic bamboos of interest, and also study the large number of herbarium specimens from that island at the Museum National d'Histoire Naturelle in July 1979.

A global view of the bamboos, which I have developed over the past decade, has given me the opportunity to examine the Sri Lanka woody bamboos in relation to those of the world, and I have been able to avoid, I hope, a provincial treatment of them. In this paper I am emphasizing the phylogenetic relationships of these bamboos and bambusoid grasses and have extended comments to make on my concepts of the genera.

In this paper I am publishing illustrations of each taxon, along with field photographs of many of the species, and micrographs of the leaf blade transectional and epidermal anatomy provided by Dr. Ellis. From this publication it will then be possible to extract the necessary information for the shorter format of the grass volume of the Flora of Ceylon.

T.R. Soderstrom
April 1987

Descriptions of some widely cultivated and economically important (or potentially important) species such as *Dendrocalamus asper* (Schultes) Backer in Heyne, *Dendrocalamus giganteus* Munro (reportedly common in the villages between Colombo and Kandy), *Dendrocalamus strictus* Nees von Esenbeck, *Bambusa polymorpha* Munro, and *Thyrsostachys siamensis* Munro were unfortunately not prepared for this treatment.

Generic delimitation in the Old World bamboos is one of the most difficult problems in agrostology, and in conversations with me before his death, Thomas R. Soderstrom stressed that the present study (which he asked me to help prepare for publication), albeit incomplete in some regards, would stimulate research in this challenging field. Therefore, it should be recognized that this paper represents only a first, tentative step towards an understanding of the bamboos of Sri Lanka.

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November 1987

The Woody Bamboos (Poaceae: Bambuseae) of Sri Lanka: A Morphological-Anatomical Study

Thomas R. Soderstrom
and Roger P. Ellis

Introduction

MATERIALS AND METHODS.—Specimens were examined from the National Herbarium of Sri Lanka in Peradeniya (PDA) and from the United States National Herbarium (US). Many of the illustrations prepared by G.B. Threlkeld were prepared from living material in Sri Lanka. The anatomical techniques used were identical to those described in Soderstrom et al. (1987).

ACKNOWLEDGMENTS.—The first author is grateful to F. Raymond Fosberg for the opportunity afforded him to carry out fieldwork in Sri Lanka as a participant in the Flora of Ceylon Project and to the Smithsonian Research Opportunity Fund that made it possible to travel to South Africa in 1983 to work in the laboratory of Roger P. Ellis. We thank Stanley Yankowski of the Smithsonian for preparing many of the leaf anatomical slides used in this study, and Alice R. Tangerini (ART) for the several fine and detailed line drawings. Thanks are also due to Mrs. Gesina Berendina Threlkeld (GBT; she appears in Figure 21*c*) who prepared illustrations in Sri Lanka for all the bambusoid species, and to the following persons for advice or assistance: the late Marie-Hélène Sachet, S.K. Jain, Sandra Kulatunge, R.B. Majumder, Julian J.N. Campbell, John Wurdack, Soejatmi Dransfield, Sally Yochelson, Mary Sangrey, and Emmet J. Judziewicz.

BAMBUSEAE Kunth

Key to the Subtribes of the Bambuseae in Sri Lanka

(an artificial key based only on the genera found on the island)

1. Spikelets not clustered or fascicled, borne in raceme- or panicle-like inflorescences; stamens 3; stigmas 2 (3 in *Arundinaria walkeriana*); mid-culm branching usually with several subequal branches . . . . ARUNDINARIINAE
1. Spikelets (pseudospikelets) clustered, borne in fascicles or capitate heads; stamens 6 or more; stigmas 3 (rarely 2 in *Dendrocalamus*); mid-culm branching variable, with either 1 or 3 main branches or many subequal branches 2
    2. Branching at midculm nodes intravaginal, with the primary branch at each node dominant; summit of ovary pubescent . . . . BAMBUSINAE
    2. Branching at midculm nodes extravaginal, with the primary branch at each node not dominant, many subequal secondary or tertiary branches branches prominent; summit of ovary glabrous . . . . SCHIZOSTACHYDINAE

Thomas R. Soderstrom, deceased, Department of Botany, Smithsonian Institution, Washington, D.C. 20560. Roger P. Ellis, Botanical Research Institute, Private Bag X101, Pretoria, South Africa.

Subtribe ARUNDINARIINAE Bentham

ARUNDINARIINAE Bentham, 1881:31.

TYPE GENUS.—*Arundinaria* Michaux, 1803:73.

DIAGNOSIS.—*Morphology:* plants erect to scandent; rhizomes sympodial, amphipodial, or monopodial; culms hollow (rarely solid), generally unarmed; primary branch buds solitary at midculm nodes, but in some taxa with several subequal branches developing; inflorescences iterauctant or semelauctant; spikelets semelauctant, 2-many-flowered, the uppermost reduced and sterile; stamens 3-6, the filaments free; ovary glabrous, with 2 or 3 stigmas; chromosome numbers $2n = 24$, 48 (generally), 54, 70-74. *Leaf anatomy:* typically bambusoid, but with midrib not as markedly asymmetric, and complex vasculature not as well developed as in other subtribes; arm cells and fusoid cells usually well developed; non-refractive cuticular papillae present, these often overarching the stomata, usually unbranched; fan-shaped groups of bulliform cells well-developed; microhairs short; silica bodies vertically oriented, narrow; epidermal prickles common.

DISTRIBUTION.—A subtribe of 12 genera of warm temperate and montane tropical regions of Asia, south-central Africa, and the southeastern United States (Soderstrom and Ellis, 1987).

Genus *Arundinaria* Michaux

Arundinaria Michaux, 1803:73.

TYPE SPECIES.—*Arundinaria gigantea* (Walter) Muhlenberg.

DIAGNOSIS.—Perennial woody bamboos with sympodial rhizomes; *culm leaves* persistent to tardily deciduous; branching intravaginal, above the nodal line; *branch leaves* with blades strongly tesselate or not. Inflorescence racemose or paniculate, often sheathed at the base by the uppermost culm leaves. *Spikelets* semelauctant, 2-several-flowered, the uppermost aborted or reduced to a rachilla segment; glumes 2, several-many-nerved; lemma 7-9-nerved; palea bicarinate; ovary with a single style and 2 (uncommonly 3) plumose stigmas. *Fruit* a caryopsis with a linear hilum as long as the fruit.

NOTE.—The above diagnosis applies only to the Sri Lanka species.

DISTRIBUTION.—For the purposes of this treatment we are treating *Arundinaria* in the very widest sense, and including elements in it that range from Sri Lanka and India to China, although the type species occurs only in the southeastern United States. All Sri Lanka species of *Arundinaria* show affinities with Chinese and Indian species that have been placed by some authors (e.g., Yi, 1983) in the segregate genus *Fargesia* Franchet (1893), which differs from *Arundinaria* sensu stricto in the following tendencies: several, evenly arranged, subequal branches at the mid-culm nodes (rather than one); sympodial rather than monopodial rhizomes; deciduous, rather than persistent sheaths; and generally paniculate rather than racemose inflorescences. The fargesioid arundinarias range from China through southern India and Sri Lanka and perhaps to Africa (*A. alpina* K. Schumann).

Key to the Species of *Arundinaria* in Sri Lanka

1. Plants scandent, vine-like.
    2. Foliage leaves narrowly oblong, 16-23 mm wide, not forming leaf complements; glumes persistent, not papyraceous; plants robust . . . . 4. ***Arundinaria scandens,*** new species
    2. Foliage leaves linear to linear-lanceolate, 3-6 mm wide, forming discrete leaf complements; glumes deciduous, papyraceous; plants delicate . . . . 1. ***Arundinaria debilis***
1. Plants erect, shrubby.
    3. Spikelets with 1 fertile floret; plants of patana bogs, the roots with air canals; foliage leaf blades tessellate below, 3.5-5 mm wide . . . . 2. ***Arundinaria densifolia***
    3. Spikelets with 2-3 fertile florets; plants of upland sites, the roots lacking air canals; blades not tessellate below, 10-50 mm wide.
        4. Spikelets 4-5-flowered, 14-20 mm long; leaves 2-5 cm wide . . . . 5. ***Arundinaria walkeriana***
        4. Spikelets 5-7-flowered, 25-35 mm long; leaves 1.0-1.7 cm wide . . . . 3. ***Arundinaria floribunda***

1. *Arundinaria debilis* Thwaites

Arundinaria debilis Thwaites, 1864:375 [type: Sri Lanka, *C. P. 1*. lectotype, PDA].—Munro, 1868:24–25.—Beddome, 1873:230–233.—Gamble, 1896:7–8, pl. 6.—Hooker f. in Trimen, 1900:311–312.—Camus, 1913:30, pl. 12.
Indocalamus debilis (Thwaites) Alston, 1931:311–312.—Senaratna, 1956:30–31.

MORPHOLOGY

FIGURES 1–3

DESCRIPTION.—Vine-like bamboo. *Culms* ~0.5–1 cm in diam., glabrous, thin-walled, spreading and hanging over other vegetation with culms developing from a sympodial pachymorph rhizome-system, the culms to 4.5 m long with primary branches to 4 m long and secondary branches to 1.5 m, the whole mass supported by trees and shrubs and hanging from them or scandent when not supported. *Culm leaves* tardily deciduous with development of branches, purplish green when young becoming stramineous, sparingly and evenly papillose-pilose; blades narrow (3–6 mm wide), reflexed-curved, 3–4 cm long, ~1/5 the length of the sheath, caducous, glabrous except for the puberulent base; ligule a short truncate pubescent rim. *Nodes* expanded upward to a ridge and marked below by the persistent basal ring-like portion of the fallen sheath, bearing a triangular bud situated above the nodal line, and covered by a prophyllum with white-pilose keels. *Branching:* central branch initiated above the nodal line with 2 secondary branches arising almost simultaneously, all 3 developing in an even row and containing several short internodes, the nodes above with buds capable of further branching. *Foliage leaves* evenly spaced and forming leaf complements of 7–10 leaves with closely overlapping sheaths; blades green above, bluish green below, linear or linear-lanceolate, narrowed abruptly at the base and gradually so above to an acuminate apex, not manifestly tessellate on either surface, hirtellous on both surfaces, sparingly so on the lower, 4–8 cm long, 3–6 mm wide, the midvein prominent on the lower surface; sheath glabrous, bearing ciliate auricles on either side of the petiole; ligule a short inconspicuous rim; petiole lacking, the base of the blade thickened at point of dehiscence with the sheath, glabrous. *Inflorescence* terminating the leafy branches a small panicle 4–6 cm long, 2–3 cm wide, with stiff ascending or spreading pulvinate branches and pedicels to 5 mm long, all parts glabrous. *Spikelets* 1–1.5 cm long, 3-flowered, the lower 2 most developed, the uppermost smallest and aborted, each separated by a narrow rachilla segment, flat and glabrous throughout or sometimes with a few cilia at the summit, narrow below and dilated upward, ~2/3 as long as the floret. *Glumes* 2, early deciduous, ovate-lanceolate, glabrous on both surfaces, the lower 7-nerved, 4–5.5 mm long, the upper 5.4–6.8 mm. *Lemma* of lowest floret ovate-lanceolate, 7–10.2 mm long, 7-nerved, glabrous; *palea* ovate-lanceolate, a little shorter than the lemma, 2-keeled, with a shallow sulcus between the keels, with a few transverse veinlets, glabrous; *lodicules* 3, ~2 mm long, rhomboid, with ciliate margins, the anterior pair slightly thickened on the lower half, many-nerved, the nerves extending almost to the tip, the posterior one fewer-nerved and shorter. *Stamens* 3, yellow, ~5 mm long, basifixed, developing before the gynecium. *Ovary* with a single style and 2 plumose stigmas. *Fruit* unknown.

DISTRIBUTION.—The species is endemic to the upper cool mountain slopes of the Central Province at elevations of 1500–2500 m.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Rangala Hill, E of Kandy, 2000 m alt., *Soderstrom & Kulatunge 1771* (US); trail to Adam's Peak from Moray Estate, *Sohmer & Sumithraarachchi 9896* (PDA, US). NUWARA EILYA DISTRICT: Hakgala, top of peak, *Alston 1027* (PDA); Pattipola, on road to Horton Plains, 1920 m alt., *Mueller-Dombois & Comanor 67070824* (PDA, US); Horton Plains at Big World's End Drop, 7000 ft. [2120 m] alt., *Davidse 7645* (PDA, US); North Cove, Bagawantalawa, 5200 ft. [1580 m] alt., 17 Sep 1904, *Farr s.n.* (PDA); Pidurutalagala, 2000 m alt., *Gould 13518* (PDA, US); Horton Plains, 2500 m alt., *Gould 13572* (PDA, US); Hakgala, 6 km E of Nuwara Eliya, 2000 m alt., *Gould & Cooray 13748* (PDA, US); Horton Plains, 2200 m alt., *Jayasuriya 2385* (PDA), *2388* (PDA); road from Kotiyagalla to Balangoda, SW monsoon country, 5600 ft. [1700 m] alt., 22 Dec 1904, *Jowitt s.n.* (PDA); in jungle N of North Cove, Bogawantalawa, 5800 ft. [1760 m] alt., 23 Dec 1904, *Jowitt s.n.* (PDA); 10 km N of Nuwara Eliya, ~1500 m alt., *Koyama 13622* (PDA); Nuwara Eliya, lower slopes of Pidurutalagala, 1890 m alt., *Soderstrom & Kulatunge 1606* (PDA, US); Nuwara Eliya Woods, 1890 m alt., *Soderstrom & Kulatunge 1612* (PDA, US); road from Diyagama Tea Estate to Horton Plains, *Sohmer & Sumithraarachchi 9992* (PDA, US); near Hakgala, *Trimen 30* (PDA); Nuwara Eliya, 1830 m, *Soderstrom 2550* (US). DISTRICT (?): Abbey Rocks [Morave Kale], 2 Mar 1881, *s. coll.* (PDA). LOCALITY UNKNOWN: *C. P. 1* (PDA, lectotype).

DISCUSSION.—On one of two sheets from PDA marked *C. P. 1*, there is a penciled annotation that reads "Maturata Aug. 1853, Ambagamuva Sept. 18[6]2, Wattekelle 18[6]5," evidently written by Trimen. We have chosen this sheet as the lectotype. There is another sheet marked *C. P. 1* but without written annotation and we can not be sure that this is the same collection. It is therefore not an isotype.

This is a locally common scandent bamboo with branches that hang from small trees and other vegetation, sometimes draping them thickly. Sporadic plants occur in flower and the species has been reported as blooming annually. This is doubtful; rather, it is likely that many years occur between the flowering of an individual and its progeny. We may be witnessing individual clumps in flower that belong to different populations. The deciduous, papyraceous glumes of the spikelet of this species are distinctive.

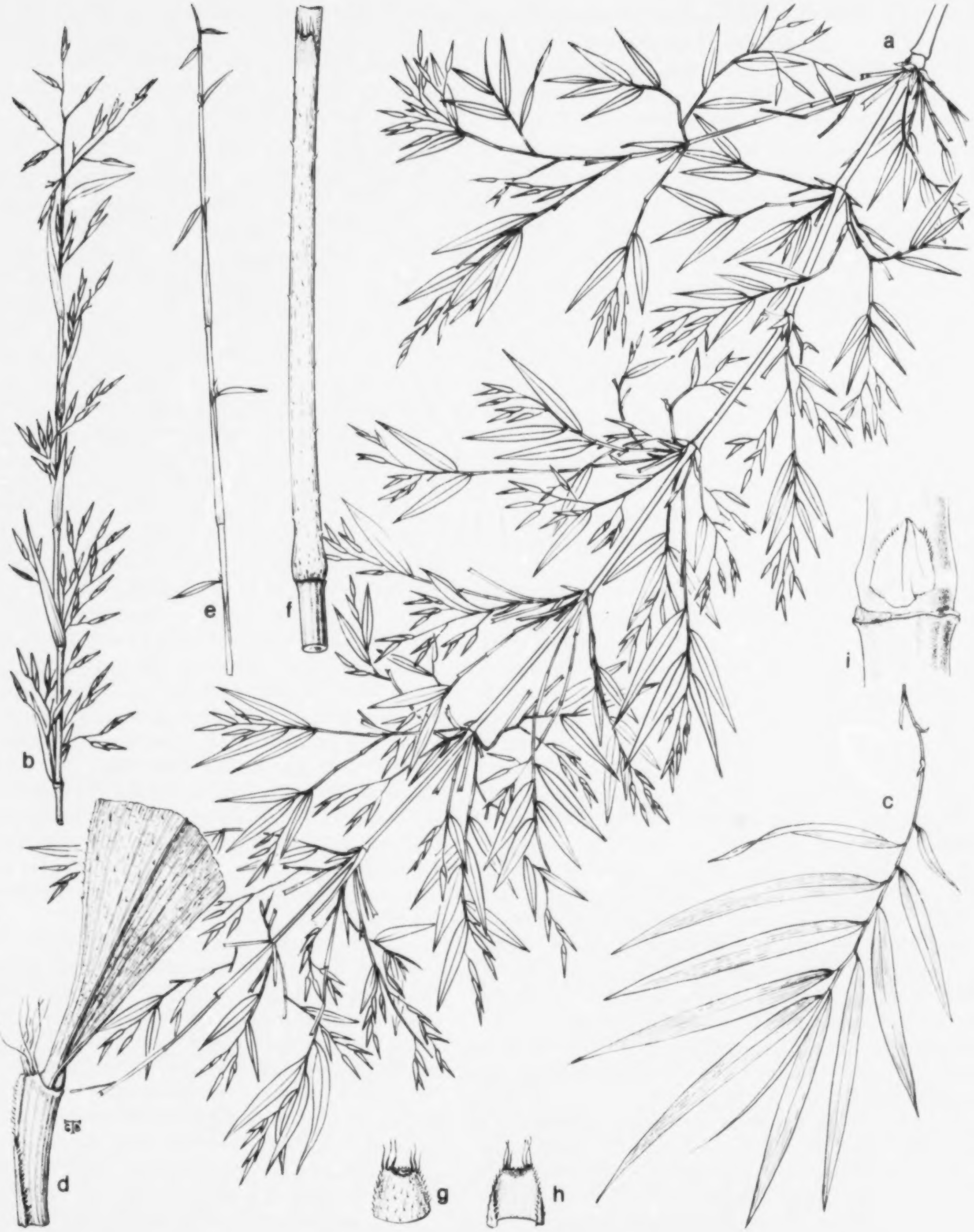

FIGURE 1.—*Arundinaria debilis: a*, flowering branch (early stage) (×0.6); *b*, flowering branch (mature stage) (×0.6); *c*, leaf complement (×0.6); *d*, leaf ligule (×7); *e*, young culm with sheaths in place (×0.6); *f*, culm with sheath (lamina abscissed) (×1.2); *g*, summit of culm sheath (outside view) (×1.2); *h*, summit of culm sheath (inside view) (×1.2); *i*, young culm bud (×3.5). (All drawings based on *Soderstrom & Kulatunge 1606.*)

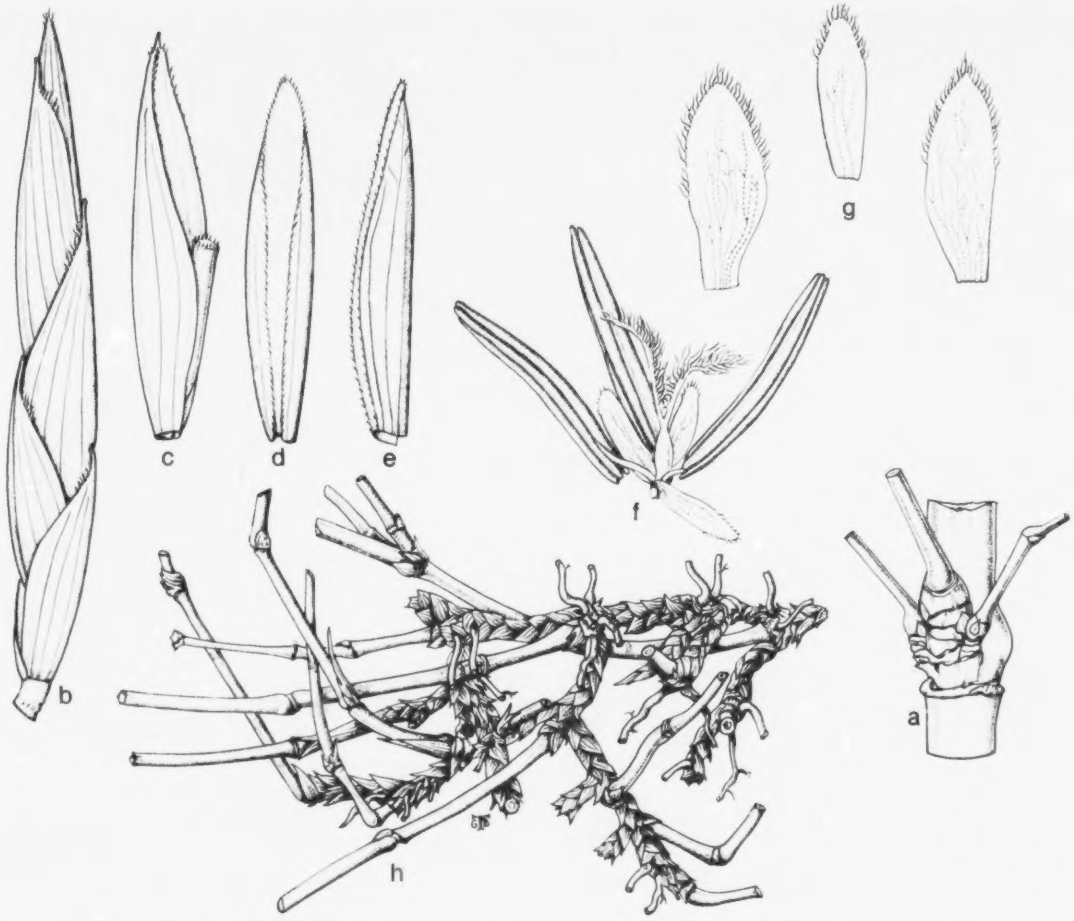

FIGURE 2.—*Arundinaria debilis: a*, branch complement (×3.5); *b*, spikelet (×3.5); *c*, lemma with rachilla (×7); *d*, palea (facing the keels) (×7); *e*, palea (lateral view) (×7); *f*, flower (×15); *h*, rhizome (×0.6). (All drawings based on *Soderstrom & Kulatunge 1606*.)

ANATOMY

FIGURE 4

DESCRIPTION.—*Leaf blade in transverse section. Outline:* expanded and flat; asymmetrical about the midrib which is strongly S-shaped (Figure 4*b*); relatively thin (~70 µm thick). *Ribs and furrows:* very shallow furrows present between vascular bundles (Figure 4*c*); one or two well-developed ribs present to one side of the midrib only (Figure 4*b*) and in the margin on the same side; other margin without prominent ribs and furrows (Figure 4*a*). *Midrib:* prominent, asymmetrical, abaxially projecting; contains three bundles, a large first order bundle abaxially situated and two smaller bundles located above this larger bundle (Figure 4*b*); all bundles embedded in sterome tissue. *Vascular bundle arrangement:* 7 first order bundles in leaf section, each separated by 5–6 third order bundles; no second order bundles. All bundles displaced slightly towards the abaxial side of the blade (Figure 4*c*). *Vascular bundle description:* third order bundles small and angular, first order bundles elliptical (Figure 4*c*); metaxylem vessels with narrow lumens, about equal to the outer bundle sheath cells in diameter; phloem adjoins the inner bundle sheath. *Vascular bundle sheaths:* double, particularly around larger bundles; elliptical. Outer sheath of third order bundles with abaxial interruption only but outer sheath absent both adaxially and abaxially around first order bundles (Figure 4*c*); no bundle sheath extensions; cells irregularly elliptical in shape, thin walled, inconspicuous, with cytoplasmic contents. Inner sheath entire, single; cells with uniformly thickened walls. *Sclerenchyma:* adaxial and abaxial girders associated with all bundles (Figure 4*c*); abaxial girders wide and shallow but adaxial girders narrow and deeper, usually only biseriate; no intercostal sclerenchyma developed; minute cap in leaf margin (Figure 4*a*). *Chlorenchyma:* fusoid cell cavities present

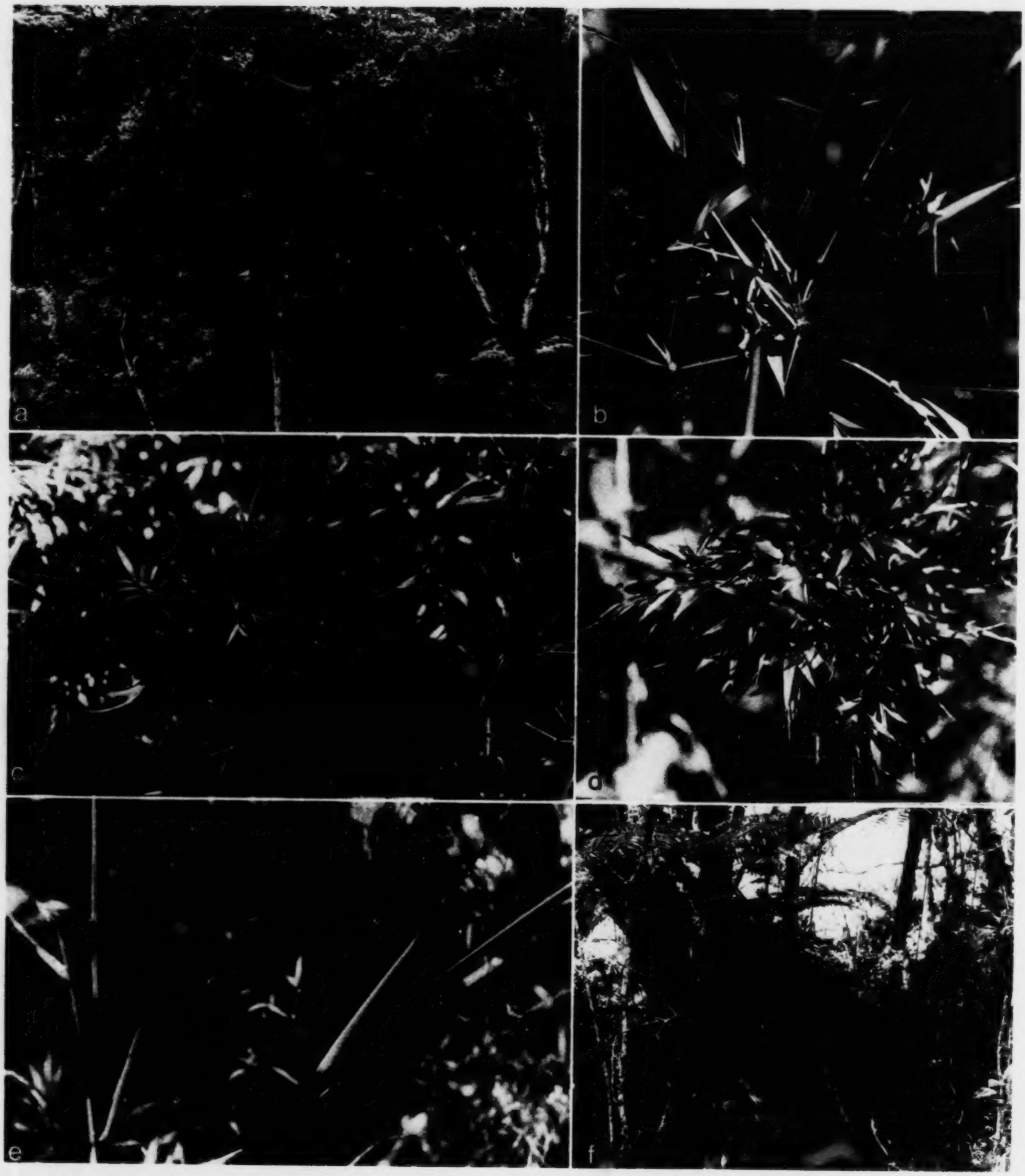

FIGURE 3.—Field photographs of *Arundinaria debilis: a*, montane woodland at Nuwara Eliya, elev. 1900 m, showing new culms among tree ferns; *b*, branching at mature node; *c*, branches, showing the delicate foliage; *d*, flowering branches; *e*, new branches, showing intravaginal branching and subtending culm sheath; the caducous blade is still attached in the young culm leaves; *f*, same habitat as in *a*, showing the sprawling nature of the thin culms. (All photographs show *Soderstrom & Kulatunge 1612*, except *c* and *d*, which are *Soderstrom & Kulatunge 1606.*)

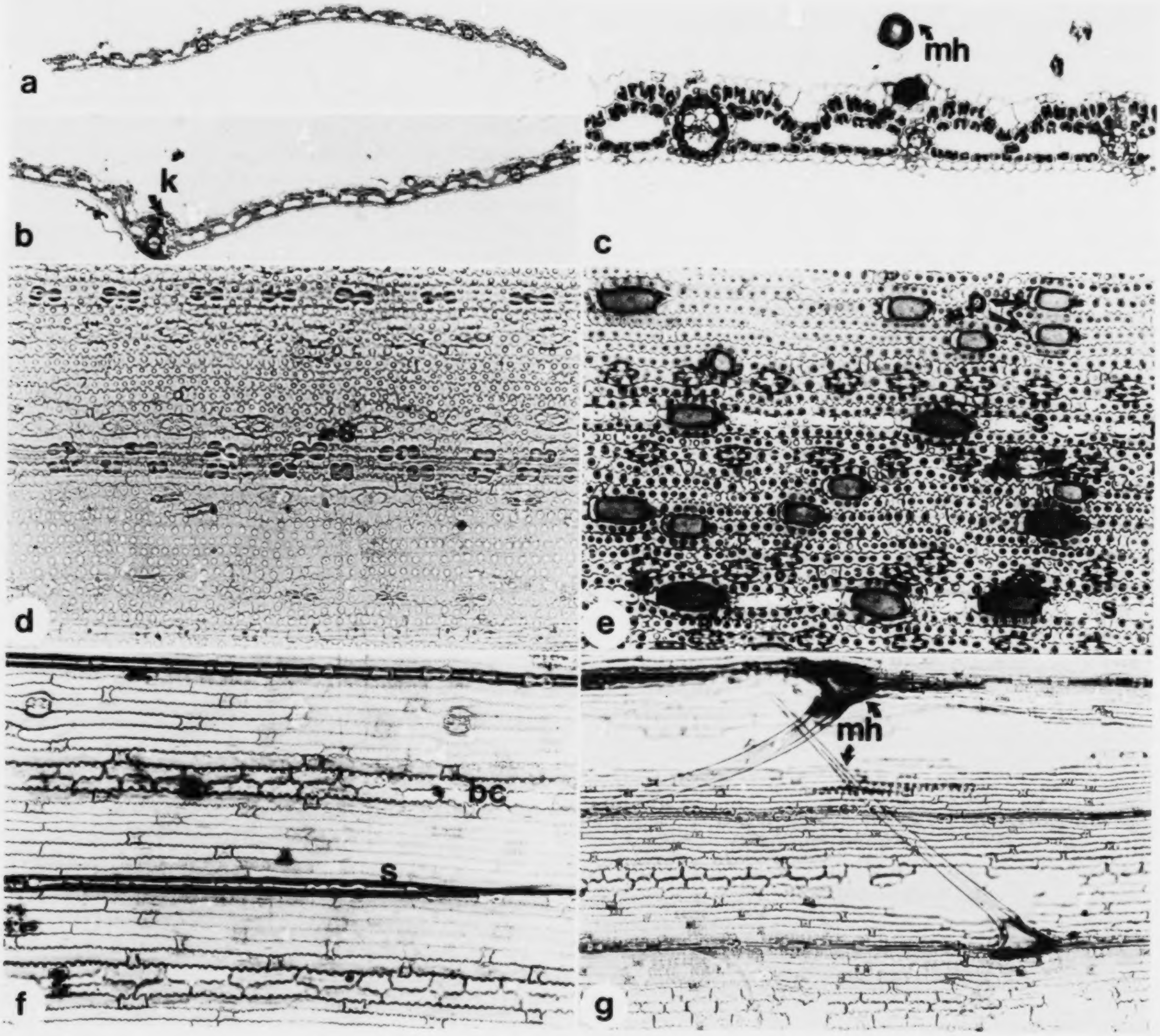

FIGURE 4.—Leaf anatomy of *Arundinaria debilis: a*, outline of lamina showing one margin (×58); *b*, outline of midrib showing keel (k) with complex vasculature embedded in sterome tissue and asymmetrical nature of blade on either side of midrib (×58); *c*, detailed lamina anatomy with fusoid cavities, three layers of arm cells and macrohair base (mh) (×230); *d*, abaxial epidermis illustrating horizontally elongated dumbbell-shaped silica bodies (s), many cuticular papillae on each long cell and stomata overarched by these papillae (×230); *e*, abaxial preparation from another part of the lamina showing presence of prickles (p) and dumbbell-shaped silica bodies (s) (×230); *f*, adaxial epidermis with files of bulliform cells (bc), dumbbell-shaped silica bodies (s), and absence of papillae (×230); *g*, adaxial epidermis with very large, unicellular macrohairs (mh) (×145). (Based on *Soderstrom 2550*.)

on both sides of all vascular bundles; elongated, horizontally oriented and abaxially located (Figure 4*c*); adjacent fusoids separated by one or two arm cells; two layers of arm cells present above the fusoid cavities and only one below; adaxially located arm cells with vertically oriented invaginations (Figure 4*c*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups fan-shaped, occupying about $^{1}/_{2}$ of the leaf thickness; central cell shield-shaped. Cuticle thin, continuous; no papillae but large macrohair bases visible (Figure 4*c*). *Abaxial epidermis:* no bulliform cells; cuticle thin; epidermal cells papillate with one papilla per cell as seen in transection; no macrohairs or prickles seen in sections.

Abaxial epidermis. Intercostal long cells: very elongated (up to 10× longer than wide), with parallel, sinuous side walls (Figure 4*d,e*); cell shape consistent throughout intercostal zones; not interspersed with short cells. *Stomata:* low dome-shaped; overarched by up to six papillae; one or two stomatal files adjacent to the costal zones; successive stomata separated by single, elongated interstomatal cell. *Intercostal short cells:* absent although bases of microhairs (Figure 4*d*) or prickles occur irregularly between intercostal long cells. *Papillae:* small, thickened, cuticular papillae present on all long cells, both costal and intercostal; 10–15 papillae arranged in a single, central row along all cells; subsidiary cells with 4–6 papillae overlapping the guard cells (Figure 4*e*). *Prickles and hooks:* either absent (Figure 4*d*) or large prickles with short barbs common in both costal and intercostal files (Figure 4*e*); both conditions occur in different parts of the same leaf. *Microhairs:* narrow and short, being the same length as the stomata (Figure 4*d*); basal cell narrow and elongated; distal cell thin-walled and deciduous; restricted to central files of intercostal zones. *Macrohairs:* absent on this surface. *Silica bodies:* costal bodies horizontally elongated, dumbbell or cross-shaped (Figure 4*d,e*); not associated with a short cell; no intercostal silica bodies. *Costal cells:* silica bodies alternate with costal long cells; long cells same width but shorter than the intercostal long cells; costal zones narrow, from 1–3 files wide.

Adaxial epidermis. Intercostal long cells: elongate rectangular, narrow with very slightly undulating side walls (Figure 4*f*); separated by single, angular to square short cell; central two files consist of bulliform cells; somewhat elongated with undulating walls. *Stomata:* absent or very rare (Figure 4*f*). *Intercostal short cells:* long cells separated by single, square to slightly rectangular short cells; appear to contain neither cork nor silica. *Papillae:* absent (Figure 4*f,g*). *Prickles and hooks:* absent. *Microhairs:* none seen. *Macrohairs:* large, unicellular, costal prickle-like with swollen bases and stiff, elongated barbs (Figure 4*g*); not associated with specialized epidermal cells; by definition these hairs are prickle hairs but because of their large size they are considered to be macrohairs. *Silica bodies:* horizontally elongated, dumbbell-shaped (Figure 4*f*). *Costal cells:* silica bodies and long cells alternate; costal zones consist of single file of cells.

SPECIMENS EXAMINED.—Soderstrom 2550, Sri Lanka, U vial no. 1960.

DISCUSSION.—The leaf transection of *Arundinaria debili* is typical of that of the Arundinariinae: the midrib, althoug rather small in size, is markedly asymmetrical and contain three vascular bundles embedded in sterome tissue; the firs order vascular bundles are surrounded by an inner bundl sheath consisting of a single layer of uniformly thickened cells and the leaf blade, although rather thin, possesses distinc fusoid cavities associated with all the vascular bundles and th arm cells have definite invaginations in their walls.

The abaxial and adaxial epidermal structure, however deviate substantially from the typical Arundinariinae type. Th exceptionally long intercostal long cells, the absence o intercostal short cells, the very short and narrow microhairs and the conspicuous, unicellular, prickle-like adaxial macrohairs are unusual in this subtribe. The horizontally elongated, dumbbell-shaped silica bodies are particularly noteworthy and deviate considerably from even the bambusoid type, although this type is also known in the arundinarioid genus *Thamnocalamus* Munro. With reference to epidermal anatomy *Arundinaria debilis* appears to link the fargesioid species of *Arundinaria* with this genus.

2. *Arundinaria densifolia* Munro

Arundinaria densifolia Munro, 1868:32 [type: Sri Lanka "Ceylon," *Watso* 25, holotype, K].—Gamble in Hooker, 1896:379.—Gamble, 1896:8–9, pl. 7.—Hooker f. in Trimen, 1900:312.—Brandis, 1906:664.—Camus, 1913:31, pl. 21c.

Chimonobambusa densifolia (Munro) Nakai, 1925:151.—Alston, 1931:342 [a *"densiflora,"* error for *"densifolia"*].—Senaratna,1956:31.

MORPHOLOGY

FIGURES 5–7

DESCRIPTION.—Dense bamboo with closely packed culm up to l cm in diam., thin-walled, erect with culms developin from a sympodial (pachymorph) rhizome system, the culm maroon to maroon-green when young, becoming yellowis brown with age, mostly 2–2.5 (–3) m tall, erect and remainin so, with primary branches usually 15–20 (rarely to 40) c long. *Rhizomes* with or without a short neck, producing thic primary roots with air cavities, and smaller, denser secondar roots, the whole mass about $^{1}/_{3}$ m deep in water. *Culm leave* persistent, indurate, appressed to culm, glabrous, stramineou disintegrating on the plant after shredded by growing branche blade erect, appressed, narrowly triangular, ~$^{1}/_{3}$ to more tha $^{1}/_{2}$ as long as the sheath; ligule a membranous rim less than 0. mm long, ciliolate on the margin. *Nodes* not expanded an marked only by a small rim left by the sheath and without a upper ridge, bearing a narrowly triangular bud situated abov the nodal line, and covered by a brown prophyllum wit

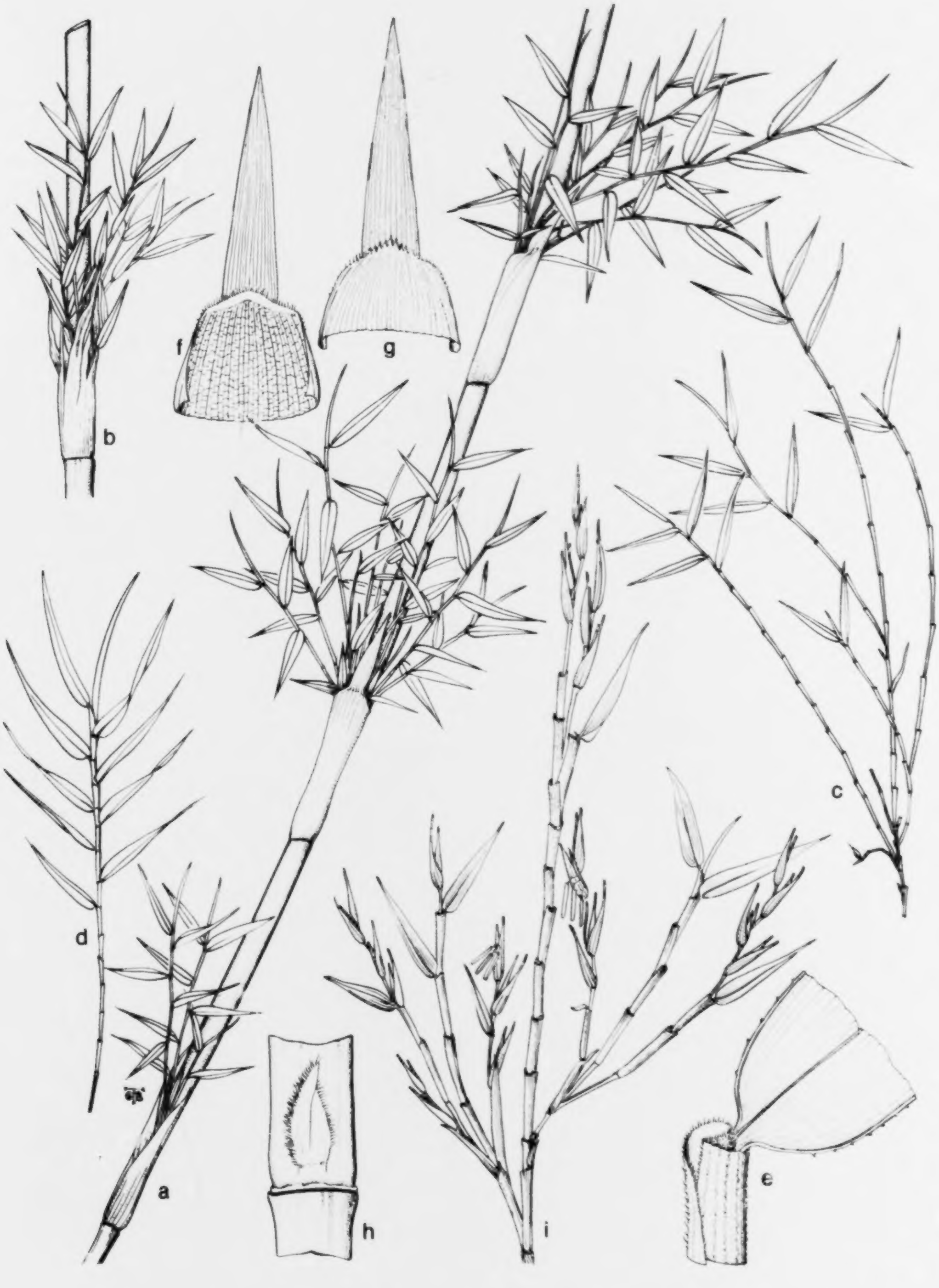

FIGURE 5.—*Arundinaria densifolia: a*, leafy branch (×0.6); *b*, whorl of branches on young culm (×0.6); *c*, branch whorl detail (×0.6); *d*, leaf complement (×0.6); *e*, leaf ligule (×7); *f*, culm sheath (inside view to show ligule) (×1.7); *g*, culm sheath (outside view) (×1.7); *h*, mid-culm bud (×1.7); *i*, flowering branches (×1.1). (Based on *Soderstrom & Kulatunge 1656*.)

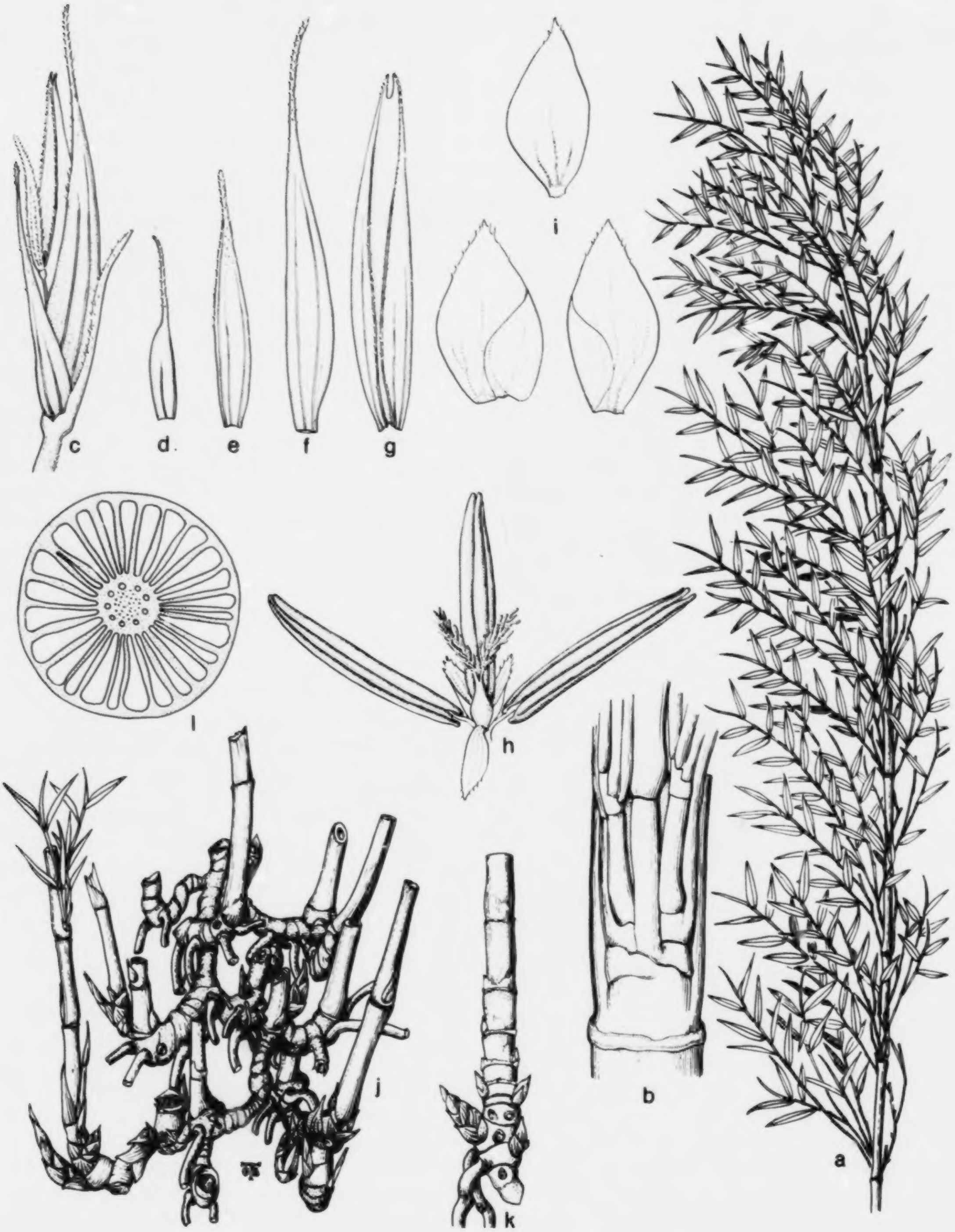

FIGURE 6.—*Arundinaria densifolia: a*, vegetative culm (×0.3); *b*, branch complement (×3.5); *c*, spikelet (×7); *d*, lower glume (×7); *e*, upper glume (×7); *f*, lemma (×7); *g*, palea (×7); *h*, flower (×7); *i*, lodicules (×15); *j*, rhizome (×0.6); *k*, rhizome bud pattern (×0.6); *l*, primary root (cross section) (×3.5). (Based on *Soderstrom & Kulatunge 1656*.)

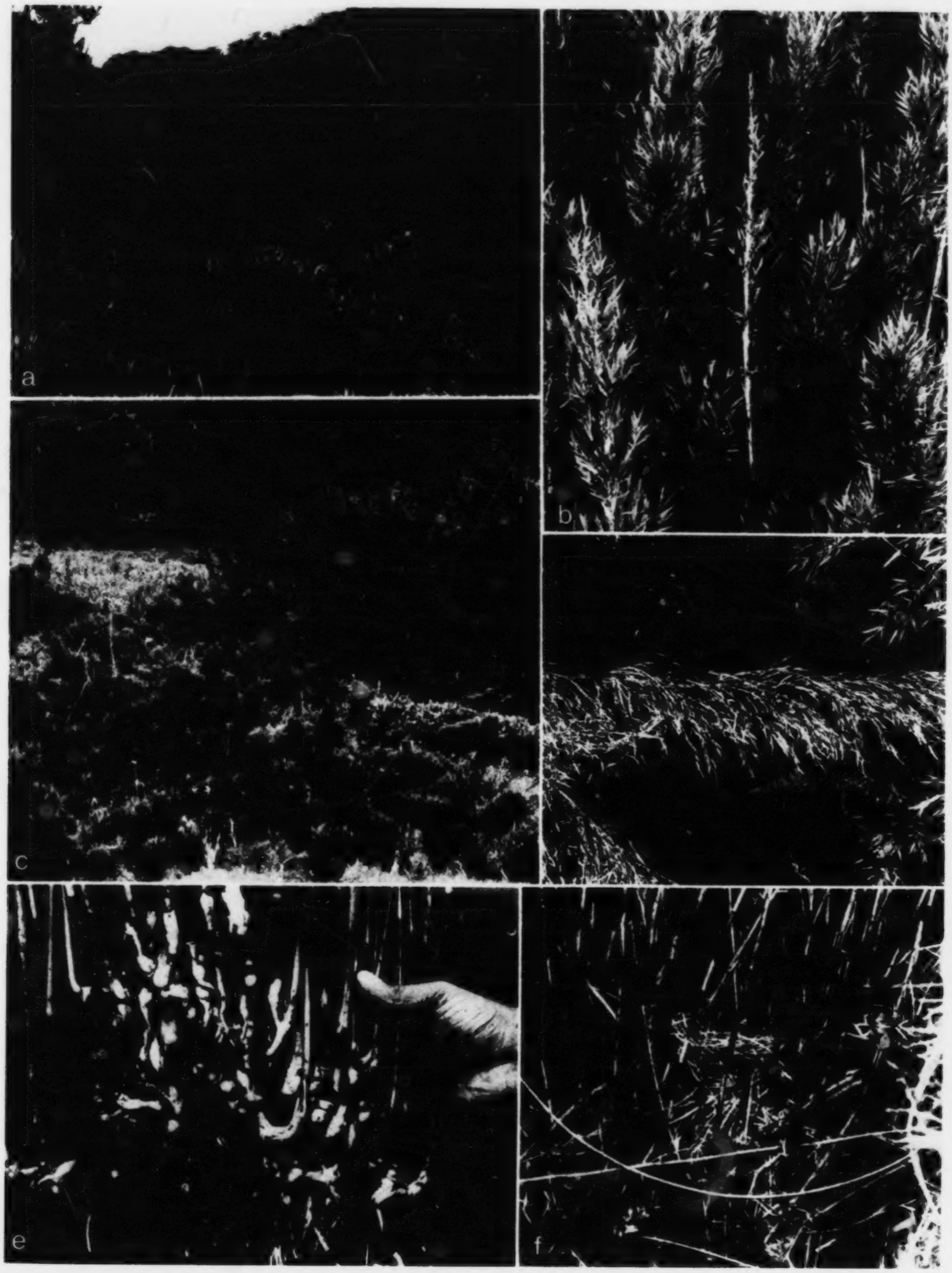

FIGURE 7.—Field photographs of *Arundinaria densifolia*, growing in pure stands on high (2200 m) swampy grassland on the Horton Plains: *a,c*, dense plumes of foliage in the lower parts of the swamp; *b*, mature leafy culms, in the center a new culm with persistent sheaths and intravaginal branching; *d*, culm in full flower; *e*, rhizomes; *f*, base of the clump showing densely placed culms. (All photographs show *Soderstrom & Kulatunge 1656*.)

white-ciliate keels. *Branching:* central branch initiated above the nodal line with 2 secondary branches arising almost simultaneously, all 3 branching in rapid succession to give rise to a cluster of many subequal branches strongly appressed to the culm, these branches without short internodes below. *Foliage leaves* forming leaf complements of 5–10 leaves with closely overlapping sheaths, the sheaths remaining below as the branch elongates and the lower blades absciss, replaced by new ones terminally; blades stiff, dull green on both surfaces, narrowly triangular with an acuminate tip, tessellate on both surfaces but not always manifest, glabrous, ~3–4 cm long, 3.5–5 mm wide, with thick cartilaginous margins, these antrorsely scabrous, the midrib elevated and prominent on the lower surface, flat and not prominent; sheath glabrous below, puberulent on the grooves toward the summit; outer ligule a tiny ciliolate rim; inner ligule a tiny ciliolate membrane, puberulent on the back; petiole glabrous, less than 1 mm long, abscissile from the thickened summit of the sheath. *Inflorescence* terminating the leafy branches, a small panicle ~3.5 cm long, 1 cm wide, with 10–15 spikelets or more often a raceme of 3 or 4 spikelets, with stiff glabrous non-pulvinate branches and pedicels up to 6 mm long. *Spikelets* purplish, ~1 cm long, 1-flowered with a rudimentary floret above or rachilla segment only, this wide below and narrowing, about half as long as the palea of the single fertile floret, the rachilla segment lying within the groove between the keels of the palea, antrorsely scaberulous. *Glumes* 2, the lower ovate-triangular, attenuate, with the single midnerve extending into a stout awn $^{1}/_{3}$–$^{1}/_{2}$ its length, glabrous below, becoming antrorsely scabrous on the awn, 4.5–6 mm long, upper glume longer than the lower, ovoid-triangular, with a short awn, glabrous except for the scabrid midnerve and awn, 7-nerved, 6–7 mm long. *Lemma* ovoid-lanceolate with an awned tip, 8–10 mm long, 7-nerved, scabrid, especially above; *palea* ovate-lanceolate, 7.5–8.5 mm long, 2-keeled, the keels close together and forming a sulcus between them, widening above and forming a flat surface, bifid at the apex, each lateral flap containing a prominent nerve, glabrous except for the scabrous keels and apex; lodicules 3, ~2 mm long, rhomboid, thickened at the base, the anterior pair with several branching vascular traces, the posterior with fewer traces, glabrous except for a few hairs at the summit. Stamens 3, pale yellowish, 4–5 mm long, basifixed. Ovary with a single style and 2 plumose stigmas. *Fruit* a brown caryopsis with a persistent style and linear hilum extending the length of the fruit.

DISTRIBUTION.—To our knowledge this bamboo is found only in the wet patanas that occur on the Horton Plains, where it often forms dense thickets and grows in cold, standing water. Gamble (1896) also cites the species from a *Beddome* collection made in 1873 on Anemudi Hill, Anamalais, but we have not seen that specimen and cannot confirm the presence of the species there.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—NUWARA ELIYA DISTRICT: Horton Plains: Reflection Lake, alt. 2300 m, *Clayton 5486* (PDA, US); along road from Pattipola, alt. 2175 m, *Comanor 451* (PDA, US); alt. 7000 ft. [2120 m], *Davidse 7600* (PDA); meadow N of Farr Inn, alt. 2300 m, *Gould & Cooray 13780* (PDA, US); alt. 7200 ft. [2180 m], 29 Aug 1902, *Jowitt s.n.* (PDA); below resthouse at Ohiya Road, alt. 2130 m, *Mueller-Dombois & Comanor s.n.* 67070915 (US); 18 Mar 1904, *Nock s.n.* (PDA); alt. 2195 m, *Soderstrom & Kulatunge 1656* (PDA,US); road from Diyagama Tea Estate to Horton Plains–Ohiya Road, *Sohmer & Sumithraarachchi 9991* (PDA), *9993* (PDA, US), *10051* (PDA); *Trimen 29* (PDA, US); 3 May 1906, "J.C.W." *s.n.* (PDA); wet grounds at base of Totapella, 17 Sep 1890, *s. coll.* (PDA). Patanas, Nuwara Eliya, 14 May 1880, *s. coll.* (PDA). World's End, Bogawanthalawa foot path, *Waas 169* (PDA, US). WITHOUT EXACT LOCALITY: "on swampy patana" in handwritten script on sheet, *C.P. 3956* (PDA); *Thwaites C.P. 3956* (US ex PDA).

DISCUSSION.—Munro had only sterile specimens at his disposal when he described this species and included material from three collectors. Of these syntypes we have chosen the first listed, *Watson 25* (K), as the lectotype. The first flowering specimens were found in 1890 at Horton Plains by Trimen, and the first complete description of the species, including vegetative and floral characters, was given by Gamble (1896).

This is one of the most reduced of the species of the genus, with the spikelet containing but a single fertile floret and a reduced floret above (or merely the rachilla segment). Some branches terminate in very small panicles but most of the inflorescences are racemes. Reduction can be seen also in the flower in which there are two stigmas, although an occasional small third one is produced. In stature *A. densifolia* approaches *Arundinaria niitakayamensis* Hayata (type species of *Yushania* Keng f.,) of southern Taiwan and northern Luzon (Philippines). The dense branches are held close to the culm, especially at the base, and the plume-like culms are close together, the whole perhaps ensuring minimal transpiration. The roots produce air canals that are typical of bamboos that occur in wet habitats (such as *Thamnocalamus tessellatus* (Nees von Esenbeck) Soderstrom & Ellis of South Africa); the dense rhizome base is found in cold water. Plants of the patanas are adapted to the reduction of transpiration and protection of new growth from intense illumination, and this bamboo follows this pattern in its densely produced foliage and thick leaves.

ANATOMY

FIGURE 8

DESCRIPTION.—*Leaf blade in transverse section. Outline:* expanded to very widely V-shaped; asymmetry not very evident about the midrib (Figure 8*a*) but left and right hand margins differ markedly in outline (Figure 8*b*,*c*); leaf thickness ~100 μm. *Ribs and furrows:* absent except slight ribs developed near one margin (Figure 8*b*). *Midrib:* comprises a

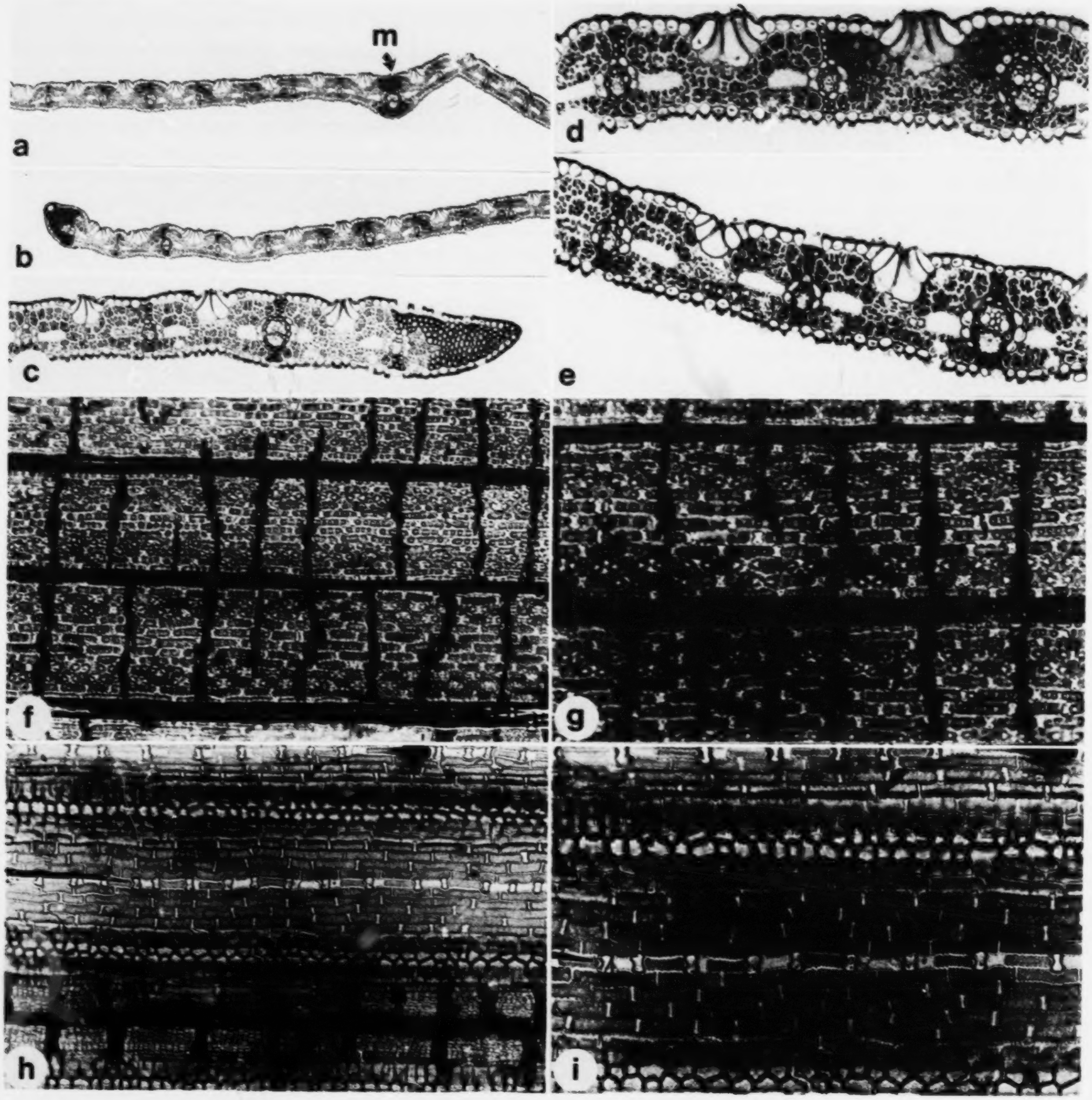

FIGURE 8.—Leaf anatomy of *Arundinaria densifolia: a,* midrib with single median bundle (m) embedded in sclerome tissue with blade not markedly asymmetrical about the midrib (×58); *b,* outline of slightly truncated margin (×58): *c,* outline of slightly tapered opposite margin (×145); *d,* detail of midlamina showing arm cell invaginations of equal length from all cell walls and irregular occurrence of fusoid cells (×230); *e,* detailed anatomy of another leaf from the same plant with bulliform groups not raised (×230); *f,* abaxial epidermis illustrating the costal (dark) and intercostal zones and regular cross veins (×93); *g,* abaxial epidermis with vertical, saddle-shaped costal silica bodies, costal and intercostal papillae and microhairs (×230); *h,* adaxial epidermal pattern of cellular arrangement (×93); *i,* adaxial epidermis with tall, narrow silica bodies and bulliform files (b) with minute papillae (×230). (Based on *Soderstrom and Kulatunge 1656.*)

single median bundle only (Figure 8*a*); embedded in sterome tissue; larger than lateral first order bundles and projecting abaxially; only slight degree of asymmetry. *Vascular bundle arrangement:* only 5 first order vascular bundles in leaf section, each separated by 3 or 4 third order bundles; no second order bundles present; all bundles slightly abaxially located (Figure 8*d,e*). *Vascular bundle description:* all bundles more or less elliptical in shape; first order bundles with thin-walled metaxylem vessels with diameters much narrower than those of the outer bundle sheath cells (Figure 8*d,e*); phloem tissue adjoins the inner bundle sheath. *Vascular bundle sheaths:* double, even around third order bundles; elliptical. Outer bundle sheaths with abaxial interruptions and adaxial interruptions on first order bundles only; no bundle sheath extensions; outer sheath cells irregularly elliptical in shape, with slightly thickened walls and without chloroplasts; laterally situated cells the largest; relatively few with 5 or 6 surrounding the third order bundles and 7 to 9 the first order bundles. Inner sheath entire, of a single layer (Figure 8*d,e*); uniformly thickened secondary walls. *Sclerenchyma:* girders associated with all bundles; narrow, biseriate; adaxial girders longer; no sclerenchyma between the vascular bundles; well-developed caps at both margins, these caps differing significantly in shape (Figure 8*b,c*). *Chlorenchyma:* non-radiate, of arm and fusoid cells; fusoid cavities small, horizontal, centrally located and of rather irregular occurrence, sometimes being absent (Figure 8*d*); adjacent fusoids separated by up to 6 mesophyll cells. Arm cells with prominent invaginations; adaxial cells without conspicuous vertical orientation of these invaginations (Figure 8*d,e*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups conspicuous, fan-shaped, occupying $^1/_3$ to $^1/_2$ the leaf thickness; sometimes raised above general level of epidermis (Figure 8*d*); without thickened cuticle; outer walls of remaining epidermal cells with distinctly thickened cuticle; no epidermal appendages visible. *Abaxial epidermis:* no bulliform cells; each epidermal cell with individually thickened cuticle projecting as cuticular papillae (Figure 8*d,e*); either single or double and with expanded ends; no hooks or prickles seen.

Abaxial epidermis. Intercostal long cells: elongated, with parallel side walls and vertical end walls; walls unthickened, slightly sinuous; detail obscured by papillae. Cell shape is consistent across intercostal zones although centrally located cells slightly larger (Figure 8*g*). *Bulliform cells* absent. Silica cells or stomata separate successive long cells. Transverse veins common (Figure 8*f*). *Stomata:* shape indistinguishable due to overlapping papillae; two files on either side of the costal zones; stomata alternate with short silica cells along stomatal files (Figure 8*g*). *Intercostal long cells:* silica cells only; tending to cross-shaped; present between all long cells in central files as well as on lateral stomatal files. *Papillae:* papillae rather large, thickened, cuticular; present on all long cells but arrangement on interstomatal long cells less regular; 4 papillae overlap the subsidiary cells. *Prickles and hooks:* absent. *Microhairs:* common in central intercostal files; basal cells only visible, elongated, at least 2× the length of the stomata (Figure 8*g*). *Macrohairs:* absent. *Silica bodies:* large, saddle-shaped along the costal zones (Figure 8*g*); cross-shaped silica bodies present between the intercostal long cells. *Costal cells:* silica bodies alternate with short costal long cells (Figure 8*g*); no cork silica cell pairs. Costal zones associated with third order bundles consist of only a single file of cells.

Adaxial epidermis. Intercostal long cells: elongate rectangular with slightly sinuous, slightly thickened walls; separated by tall and narrow silica cells (Figure 8*i*). Central two files consist of short, hexagonal bulliform cells alternating with adjacent row; not silicified. *Stomata:* absent. *Intercostal short cells:* tall, narrow silica cells between all long cells; much narrower than costal silica cells (Figure 8*h,i*). *Papillae:* absent on all cells except the outer tangential walls of the bulliform cells which have very small cuticular papillae (Figure 8*i*); no refractive micro-papillae present. *Prickles and hooks:* absent. *Microhairs:* apparently absent from this surface. *Macrohairs:* absent. *Silica bodies:* costal bodies vertically elongated, saddle-shaped; intercostal bodies very narrow and tall (Figure 8*h,i*). *Costal cells:* costal zones consist of a single row of cells; alternating silica cells and rectangular long cells (Figure 8*i*).

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1656*, Sri Lanka; US vial no. 436.

DISCUSSION.—The small fusoid cavities, which are sometimes even lacking, are a characteristic that is not unusual in the Arundinariinae. The only noteworthy departure from classical arundinarinoid anatomy are the abaxial papillae, which have expanded or bifurcating ends, a feature more typical of the Bambusinae.

3. *Arundinaria floribunda* Thwaites

Arundinaria floribunda Thwaites, 1864:375 [type: Sri Lanka, "Maturatte District," 5000 ft. [1520 m] alt., *Thwaites s.n.*, in 1853, *C. P. 2624*, holotype, PDA].—Munro, 1868:20.—Beddome, 1873:230.—Gamble, 1896:5–6, pl. 3.—Gamble in Hooker, 1896:377–378.—Hooker f. in Trimen, 1900:310–311.—Camus, 1913:28–29, pl. 16B.

Indocalamus floribundus (Thwaites) Nakai, 1925:148.—Alston, 1931:342.—Senaratna, 1956:30.

MORPHOLOGY

FIGURES 9–11

DESCRIPTION.—Shrubby bamboo of erect culms from sympodial, pachymorph rhizomes, with hollow culms to 2.5 m tall, the internodes light green and mottled with purplish black specks when young, roughened, especially toward the summit bearing a ring of purple hairs when young, the older culms lighter in color and smooth. *Culm leaves* deciduous, the sheath light green flushed with maroon, sparsely hirsute throughout with maroon hairs, becoming stramineous, pushed off by developing branches and leaving a small glabrous ring of tissue at the base; blade soon abscissile, ~3 cm long, 2–3

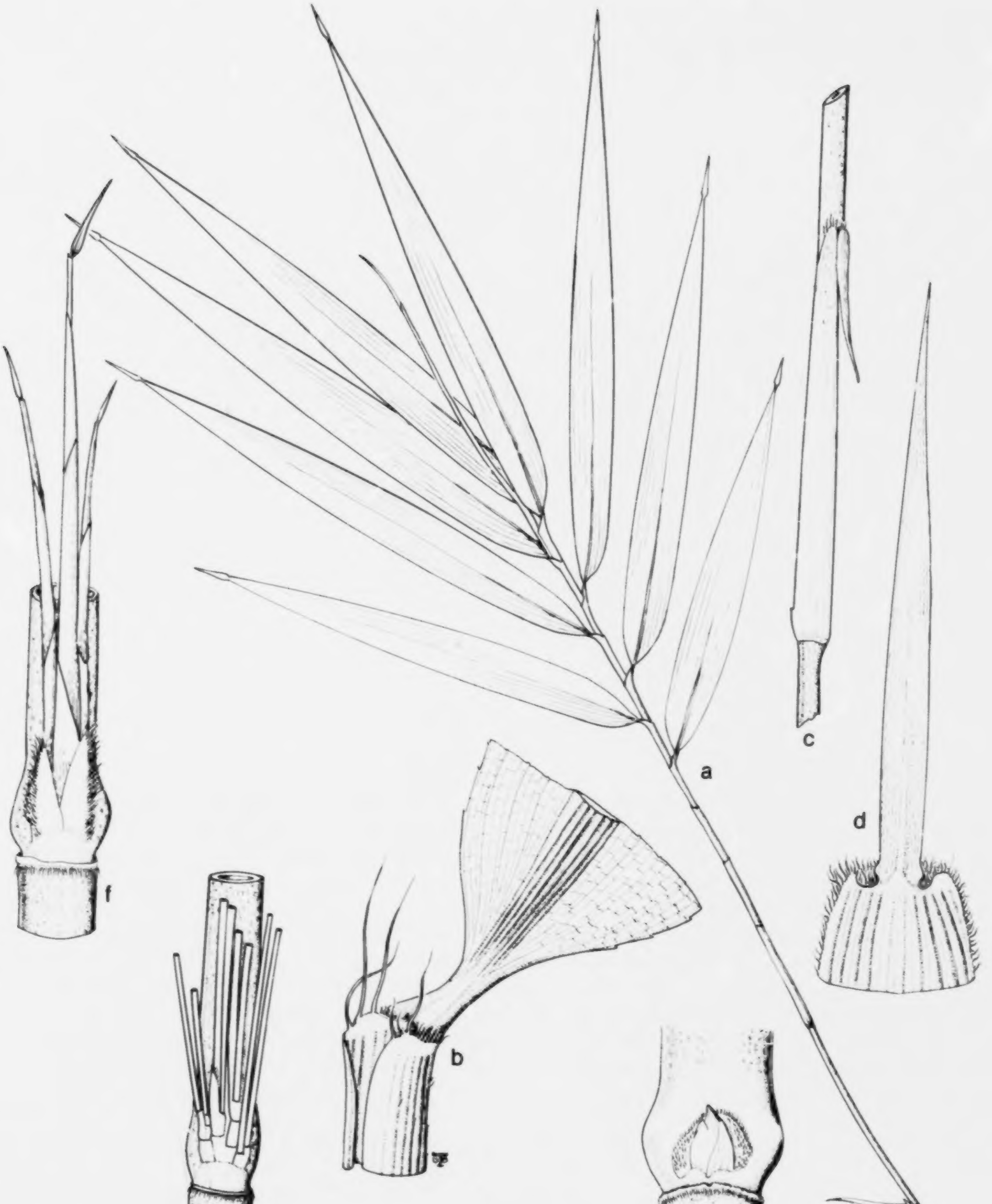

FIGURE 9.—*Arundinaria floribunda*: *a*, leaf complement (×0.6); *b*, leaf ligule (×3.5); *c*, culm sheath in place (×0.6); *d*, culm sheath (outside view) (×3.5); *e*, bud on young culm (×1.7); *f*, branching, early stage (×1.7); *g*, branch complement (×1.7). (Based on *Soderstrom & Kulatunge 1658*.)

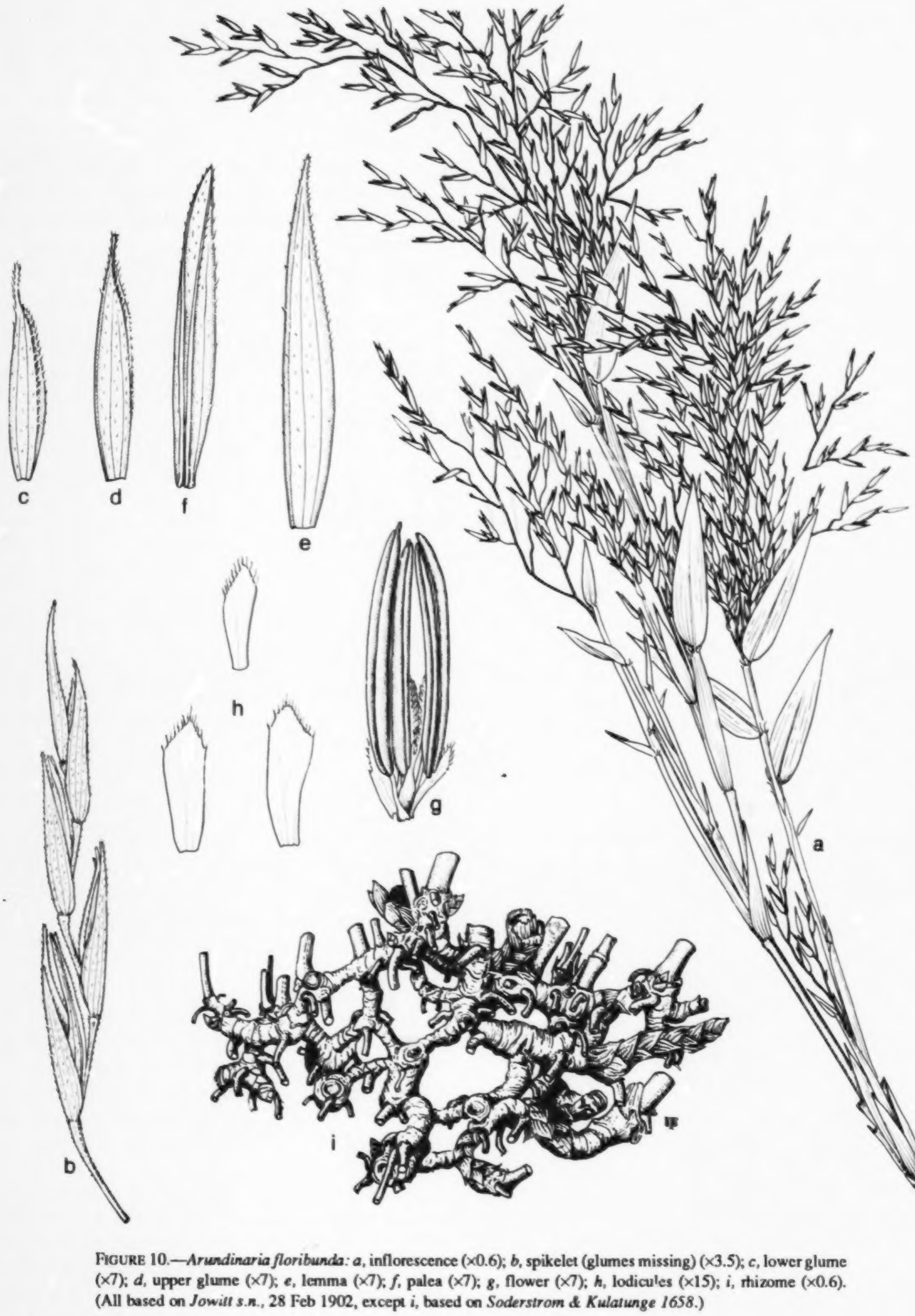

FIGURE 10.—*Arundinaria floribunda: a*, inflorescence (×0.6); *b*, spikelet (glumes missing) (×3.5); *c*, lower glume (×7); *d*, upper glume (×7); *e*, lemma (×7); *f*, palea (×7); *g*, flower (×7); *h*, lodicules (×15); *i*, rhizome (×0.6). (All based on *Jowitt s.n.*, 28 Feb 1902, except *i*, based on *Soderstrom & Kulatunge 1658*.)

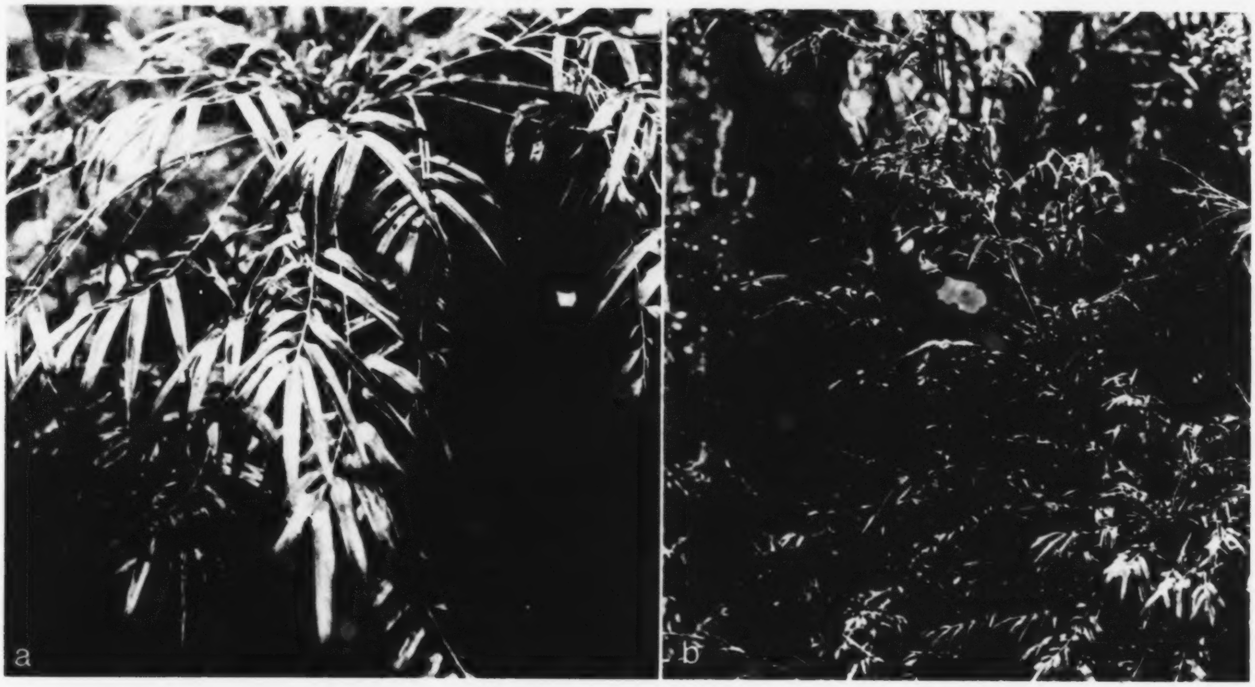

FIGURE 11.—Field photographs of *Arundinaria floribunda*, in woods between Ohiya and Burlanda, Badulla District, at 1890 m elev.: *a*, foliage; *b*, plants. (Photographs show *Soderstrom & Kulatunge 1658*.)

mm wide, ~$^{1}/_{3}$–$^{1}/_{4}$ the length of the sheath, linear-lanceolate, with a truncate base narrower than the sheath and an acuminate tip, erect at first, becoming horizontal or reflexed; ligule a short membrane ~0.5 mm long, puberulent abaxially. *Nodes* containing a single branch bud. *Branching:* central branch and two laterals developing more or less simultaneously, followed by other branches from these axes to form a whorl of usually 5 more or less equal branches, the latter occasionally rebranching but at maturity the whole branch complement not crowded, the branches continuing in length with usually 6–10 leaves in the terminal complement, the lower part of the branch consisting of only hard, persistent, overlapping sheaths. *Foliage leaves* glabrous, the blades 9–18 cm long, 1–1.7 cm wide, lanceolate, narrowed abruptly at the base and extending terminally into an acuminate tip, the midvein prominent especially on the lower surface, the margins thin, glabrous or sparingly antrorsely scabrous, transverse veinlets manifest on both surfaces; sheath summit fimbriate on either side of the short petiole and ciliolate between (outer ligule); ligule a short rim not manifest, petiole hardly differentiated, represented by the gradually narrowed base of the blade. *Inflorescence* terminating the branches a large spreading panicle ~15–20 cm long, 8–10 cm wide, the branches glabrous and with pulvini on the upper surface at the axil, the pedicels 7–8 mm long, each bearing a many-flowered spikelet. *Spikelets* purplish, 2.5–3.5 cm long, usually 5–7-flowered, the lowest floret longest and most complete, the uppermost smallest and aborted, each separated by a narrow rachilla segment flat and glabrous at the base becoming pubescent upward and short-pilose on the upper half, the hairs especially dense on the rim at its juncture with the anthecium. *Glumes* 2, the lower 3.8–5.6 mm long, ovate-triangular, glabrous, with a few cilia on the upper edges, 5-nerved, the upper 5.5–6.1 mm long, ovate-lanceolate, glabrous, with a few cilia on the upper edge, 7-nerved. *Lemma* of lower florets 8.5–10 mm long, ovoid-lanceolate with an apiculate tip, 7- or 8-nerved with some transverse veinlets, scabrous; *palea* a little longer than the lemma, with 2 keels and 2 broad wings, each with 1 or 2 nerves, sulcate between the keels, bifid at the apex, scabrid, especially toward the summit; *lodicules* 3, 1.5–2 mm long, the anterior pair rhomboid and narrowed at the base, the posterior lanceolate, all ciliate on the apex, thickened at the base, many-nerved; *stamens* 3, the anthers orange-yellow, basifixed, 4.3–6 mm long; *ovary* not found. *Fruit* unknown.

DISTRIBUTION.—Endemic to the mountains of south-central Sri Lanka.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—BADULLA DISTRICT: Pita Ratmalie, Haptule, 6000 ft. [1820 m] alt., 28 Feb 1902, *Jowitt s.n.* (PDA) and 7 Feb 1903, *Jowitt s.n.* (PDA); between Ohiya and Boralanda, 1890 m alt., *Soderstrom and Kulatunge 1658* (US). RATNAPURA DISTRICT: NE of E and W boundary near 13th mile post from Kotiyagalla to Balangoda, 5600 ft. [1700 m] alt., 22 Dec 1904, *Jowitt s.n.* (PDA). NUWARA ELIYA DISTRICT: Haputala Range, near

Ohiya, *Soderstrom 2555* (US). DISTRICT NOT GIVEN: top of Naminabuli, *Willis 103* (PDA, US). LOCALITY UNKNOWN: "Maturatte District," 5000 ft. [1520 m] alt., *Thwaites s.n.* in 1853, *C.P. 2624* (Holotype, PDA).

DISCUSSION.—*Arundinaria floribunda* forms small clumps with culms 2–3.5 m tall, these somewhat scabrous and speckled with purplish markings; the nodes are especially thick, flaring upward to a prominent ridge. In our own collection of this species (*Soderstrom and Kulatunge 1658*), the clumps were scattered throughout the closed forest with *Cupressus*, not occurring in abundance anywhere. On a return trip to the area in 1978, much of the region had been given over to reforestation and most of the bamboo population was gone.

A few sterile specimens have a combination of features that is not found in any of the described species of the genus from Sri Lanka or southern India. These specimens have compressed-keeled sheaths, a large glabrous ligule without oral setae, a glabrous ring representing the base of the fallen sheath, violet culms, and blades with thick cartilaginous margins that are antrosely scabrous. Previously referred to *A. floribunda*, they appear distinct enough to warrant specific status, but we only draw attention to them here, awaiting more complete material: Adam's Peak, Aug 1869, *C.P. 4023* (PDA); near Gatmore Estate, Maskeliya, Rasamaliya, 29 Apr 1926, *Silva s.n.* (PDA). Referring to the former collection, Trimen (1900) remarked that "specimens collected on Adam's Peak, numbered C. P. *4023*, Aug. 1869, by Dr. Thwaites, in leaf only, may belong to this species [*F. floribunda*]." It is interesting that he could not place these specimens in *A. floribunda* with confidence.

ANATOMY

FIGURE 12

DESCRIPTION.—*Leaf blade in transverse section. Outline:* expanded, asymmetrical with the lamina on either side of the midrib being S-shaped (Figure 12*a*) and with the two margins differing in outline (Figure 12*c,d*); leaf thickness ~90 µm. *Ribs and furrows:* very shallow furrows present above all bulliform cell groups; slight ribs present on one side of midrib (Figure 12*a*) and near margin on same side (Figure 12*c*). *Midrib:* abaxially projecting, broadly S-shaped, asymmetrical structure (Figure 12*a*); vasculature complex with single abaxially located first order bundle flanked by two third order bundles and a further two third order bundles situated towards the adaxial side; all bundles embedded in sclerechyma fibers. *Vascular bundle arrangement:* 9 first order bundles in transection; six third order bundles between successive first order bundles; all bundles located closer to the abaxial than the adaxial surface (Figure 12*b*). *Vascular bundle description:* third order bundles vertically elliptical and first order bundles round in shape (Figure 12*b*); metaxylem vessels distinct, wider than the outer bundle sheath cells, unthickened; phloem adjoins the inner bundle sheath. *Vascular bundle sheaths:* double; elliptical or round; with abaxial interruptions only; interruptions of first order bundles very wide, extending right around the phloem tissue (Figure 12*b*); no outer sheath extensions; outer sheath cells small, indistinct, with thin walls and cytoplasmic contents. Inner sheath entire, single; cells with uniformly but heavily thickened walls (Figure 12*b*). *Sclerenchyma:* adaxial and abaxial girders associated with all the bundles; abaxial girders well developed, trapezoidal and narrowing towards the bundles; adaxial girders smaller and narrower. No sclerenchyma between the bundles. Small sclerenchyma caps present in margin; shape of two margins very different (Figure 12*c,d*). *Chlorenchyma:* fusoid cell cavities present on either side of all bundles, even those located near the margins (Figure 12*c,d*); wide and horizontally orientated (Figure 12*b*); adjacent fusoids separated by one or two chlorenchyma cells. Arm cells with well-developed invaginations in all cells, the adaxially situated cells with these invaginations vertically orientated (Figure 12*b*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups fan-shaped, situated at the bases of shallow furrows; occupy less than half the leaf thickness. Outer wall of other epidermal cells with continuous cuticle; no macrohairs or papillae but prickle bases present (Figure 12*b*). *Abaxial epidermis:* no bulliform cells; epidermal cells with continuous cuticle and without papillae; no macrohairs but prickle bases present.

Abaxial epidermis. Intercostal long cells: elongated rectangular, particularly the central files where length may be 10× greater than cell width; side walls parallel, unthickened, and sinuous; cell shape differs across intercostal zones with central cells being much longer (Figure 12*f*). No bulliform cells. Short cell pairs, stomata, microhairs or prickles separate successive long cells. *Stomata:* low dome-shaped; flange-like papillate outgrowths from the subsidiary cells conceal guard cells beneath a cross-shaped opening (Figure 12*f*); three rows of stomata on either side of each costal zone, i.e., six per intercostal zone; stomatal files adjacent to one another; one interstomatal cell between successive stomata in a file. *Intercostal short cells:* paired in central files; silica cell tall and narrow and cork cell square to tall and narrow (Figure 12*f*) present between all long cells in these central files except where hooks or microhairs emerge. *Papillae:* absent except for papillate outgrowths on the subsidiary cells. *Prickles and hooks:* small hooks with short barbs present on central intercostal files; no costal prickles. *Microhairs:* elongated finger-like; total length of hairs about 4× length of the stomata; basal and distal cells about equal in length; distal cell thin walled and indistinct; basal cell with thicker wall and arises from a short cell (Figure 12*f*); present on the central intercostal files and immediately adjacent to the costal files. *Macrohairs* absent. *Silica bodies:* tall saddle-shaped in costal zones; tall and narrow in intercostal zones (Figure 12*f*); shape rather irregular. *Costal zones:* cork-silica cell pairs alternate with elongated, rectangular long cells along costal zones (Figure

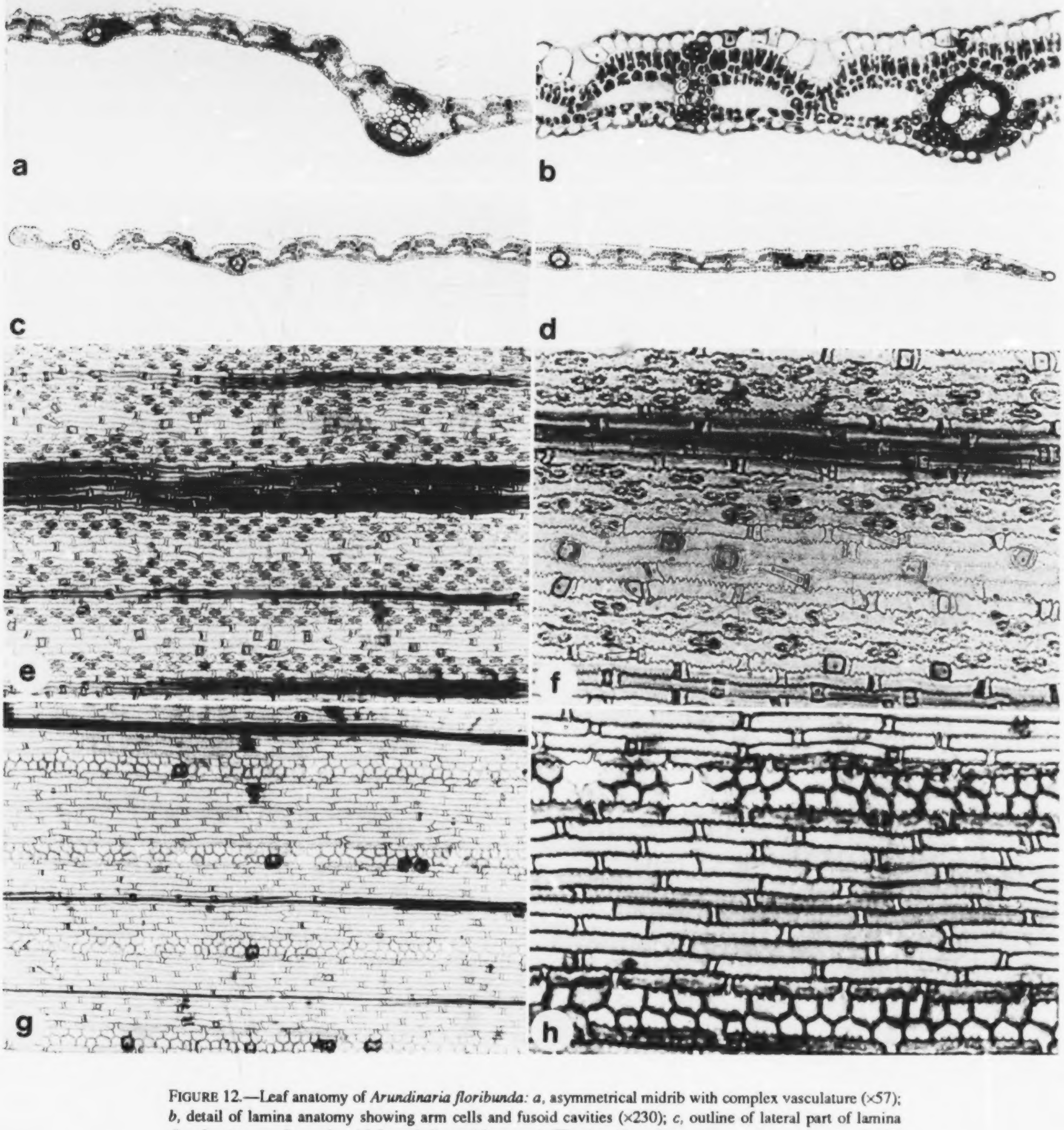

FIGURE 12.—Leaf anatomy of *Arundinaria floribunda*: *a*, asymmetrical midrib with complex vasculature (×57); *b*, detail of lamina anatomy showing arm cells and fusoid cavities (×230); *c*, outline of lateral part of lamina showing truncated margin with lateral ribs and furrows (×57); *d*, outline of tapering margin not associated with ribs from the opposite side of the lamina (×57); *e*, costal and intercostal zone distribution on abaxial epidermis (×9); *f*, costal flanges, microhairs, hooks, and silica bodies on abaxial epidermis (×230); *g*, adaxial epidermis with dark, silicified bulliform cells (×90); *h*, adaxial epidermis showing files of bulliform cells and similarity in cell pattern between costal and intercostal zones (×230). (Based on *Soderstrom 2555*.)

12*f*); third order bundle costal zones 3–4 cell files wide but first order bundles with up to 12 costal cell files (Figure 12*e*).

Adaxial epidermis. Intercostal long cells: elongate rectangular with very slightly sinuous walls (Figure 12*h*); separated by single short cell; central four files of each zone consist of shorter, angular bulliform cells arranged in an interlocking manner; may be silicified (Figure 12*g*). *Stomata:* absent. *Intercostal short cells:* single, vertically elongated short cell between all long cells (Figure 12*h*). *Papillae:* absent. *Prickles and hooks:* absent on preparations examined. *Microhairs:* absent. *Silica bodies:* tall and narrow; very few present. *Costal zones:* very narrow, consisting of one or two files only; cells indistinguishable from the lateral files of the intercostal zones (Figure 12*h*); silica bodies solitary.

SPECIMEN EXAMINED.—*Soderstrom 2555*, Sri Lanka; US vial no. 1967.

DISCUSSION.—The abaxial epidermis is atypical of the Arundinariinae in that there are no epidermal papillae. The stomata are, consequently, not obscured by papillae and, instead, flange-like outgrowths from the subsidiary cells conceal the guard cells. The microhairs are extremely long, at least four times as long as the length of the stomatal complexes.

Arundinaria floribunda deviates from the anatomical diagnosis of the subtribe in the absence of epidermal papillae and this deserves further comment. The leaf transverse sections confirm that papillae do not occur anywhere across the width of the leaf blade. The other *Arundinaria* species from Sri Lanka all possess well-developed papillae. This type of pattern of variation is common in the Bambuseae, where specific differences may be greater than generic or even subtribal differences. No anatomical characters appear to separate the genera of the Arundinariinae and it appears as if individual genera and species cannot be recognized on leaf anatomy alone.

4. *Arundinaria scandens* Soderstrom & Ellis, new species

Arundinaria sp. nov. a *A. debilis* Thwaites similis sed plus robustus, foliae angustiore (16–23 mm latae) et non complementae formans, et glumae persistentae non papyraceae.

TYPE SPECIMEN.—SRI LANKA: summit of Pidurutalagala [as "Pedro-tala-galla"], Sep 1881, *Beddome s. n.* (Holotype, PDA).

MORPHOLOGY

FIGURES 13, 14

DESCRIPTION.—Scandent bamboo forming dense clumps of 100–200 culms arising from a sympodial system of pachymorph rhizomes, the culms 7–8 m long, ~1.5 cm in diameter, hollow with thick walls, at first erect, then arching and scandent, purplish green and hirsute with white hairs when new, becoming glabrous or scabrid with age and green or purplish green. *Culm leaves:* sheath persistent, at first purplish or dark maroon with broad lighter-colored margins, sparingly to densely hirsute with dark brown appressed hairs, becoming lighter tan with age; blade 10–12 mm long, 2.5 mm wide, deciduous, narrowly oblong, acute at the apex, antrorsely scabrous, horizontal or horizontal-ascending, $^{1}/_{8}$–$^{1}/_{10}$ as long as the sheath; ligule a rounded membrane ~1.7 mm long with an irregularly toothed margin. *Nodes* thickened by the expanded hirsute base of the sheath, containing a single narrowly triangular branch bud covered by a prophyllum with dark brown pilose keels. *Branching:* central branch initiated above the nodal line giving rise to a branch at each of its evenly spaced nodes with 3 or 4 secondary branches developing shortly after the main axis has elongated, the secondary branches in turn producing tertiary branches at their nodes, the whole ultimately resulting in a dense cluster of long widely divergent branches, enveloped at the base by the persistent sheath, the primary branch reaching as much as 2 m in length. *Foliage leaves* somewhat evenly spaced and not forming discrete leaf complements with closely overlapping sheaths; blades green above, bluish green below, narrowly oblong, with a rounded base and acute pointed tip, strongly tessellate on both surfaces, glabrous, 6–9 cm long, 1.6–2.3 cm wide, smaller on the higher orders of branches, the blade with a prominent midvein and smooth margins except at the sparingly scabrid base; petiole very short, hardly developed, glabrous; ligule an inconspicuous, irregular toothed membrane ~0.5 mm long, glabrous; petiole thick, glabrous, ~0.5 mm long. *Inflorescence* terminating the branches an open panicle 6–7 cm long, ~6 cm wide with stiff spreading or ascending branches, each branch and pedicel pulvinate above, all parts glabrous, the pedicels up to 2 cm long. *Spikelets* purplish, ~12 mm long, usually 3-flowered, the lower 2 florets longest and most developed, the uppermost smallest and aborted, each separated by a narrow rachilla segment flat and glabrous below, dilated upward and appressed white-pubescent on the expanded portion, $^{1}/_{2}$–$^{2}/_{3}$ as long as the floret, the hairs longer on the summit at its juncture with the anthecium. *Glumes* 2, ovate-triangular and narrowing to an abrupt apex, glabrous on the outside, puberulent on the inner surface on the upper part, 5-nerved with a few transverse veinlets, the 1st glume 2.7–3 6 mm long, the 2nd 3.9–4.5 mm long. *Lemma* of lowest floret 6.3–7.5 mm long, ovoid-lanceolate, 7-nerved, glabrous on the outside, puberulent on the inner surface on the upper part; *palea* a little shorter than the lemma, broad, truncate at the apex, strongly 2-keeled and winged, with 2 nerves in each wing and 3 between the keels, puberulent between the keels dorsally, otherwise glabrous *lodicules* 3, 1.6–1.7 mm long, the 2 anterior broad with an acute apex and ciliate margins, the posterior a little smaller. *Stamens* 3, ~5 mm long. *Ovary* with 2 stigmas. *Fruit* unknown.

DISTRIBUTION.—Endemic to Sri Lanka, where known only from the summit of Pidurutalagala, where it occurs from about 2100 m to the summit (2500 m).

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—NUWARA ELIYA DISTRICT: Pidurutalagala, *Soderstrom & Kulatunge*

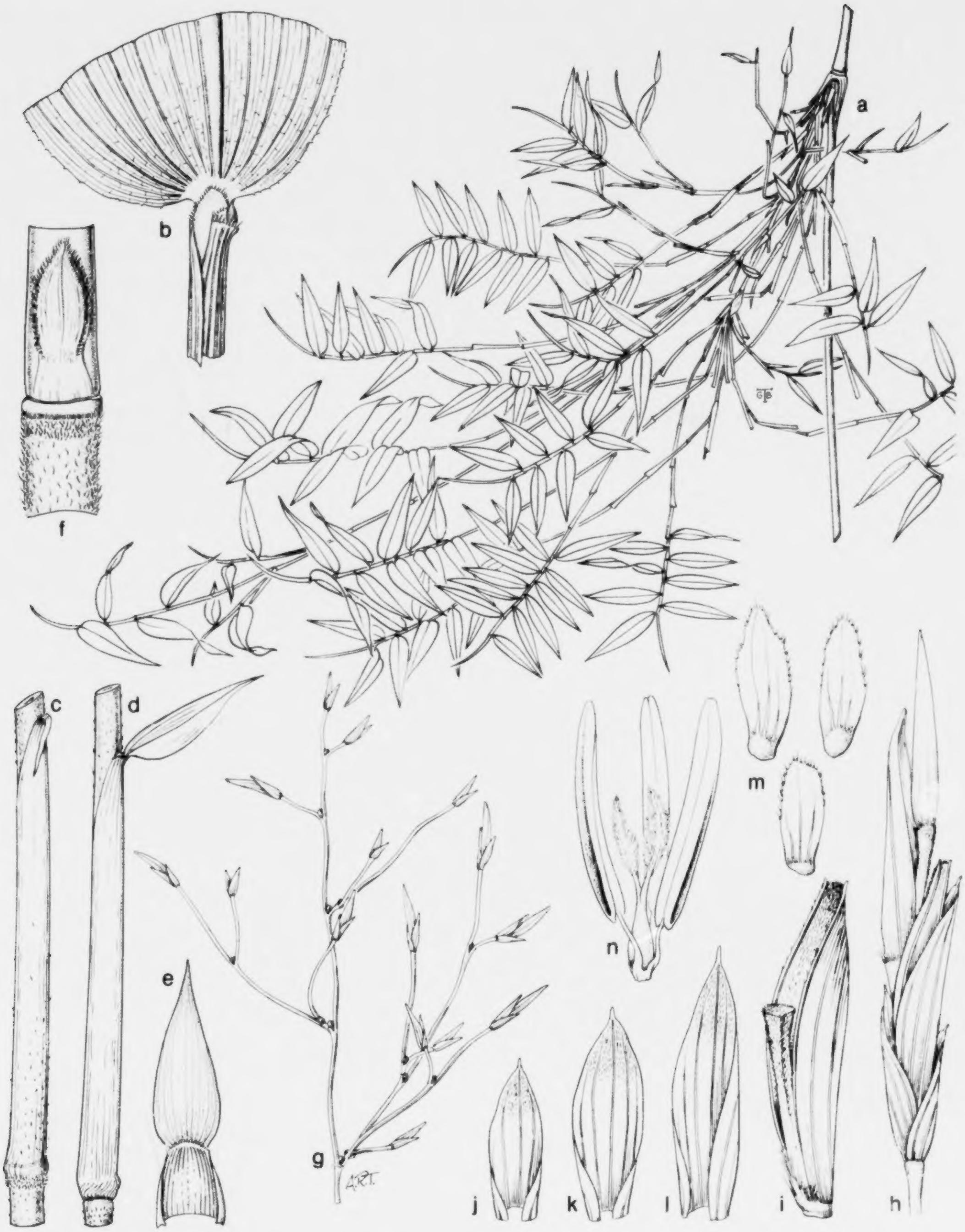

FIGURE 13.—*Arundinaria scandens* Soderstrom & Ellis, new species: *a*, leafy branch habit (×0.3); *b*, foliage leaf ligule (×3.4); *c*, young culm sheath in place (×0.6); *d*, older culm sheath in place (×0.6); *e*, culm sheath, adaxial view to show ligule (×0.6), *f*, young culm bud (×1.1); *g*, inflorescence (×1.1); *h*, spikelet (×7); *i*, floret, showing palea and rachilla segment (×8.5); *j*, lower glume (×8.5); *k*, upper glume (×8.5); *l*, lemma (×8.5); *m*, lodicules (×14); *n*, andrecium and gynecium (×8.5). (Illustrations *a–f* based on *Soderstrom & Kulatunge 1608*, *g–n* on *Beddome s.n.*, Sep 1881.)

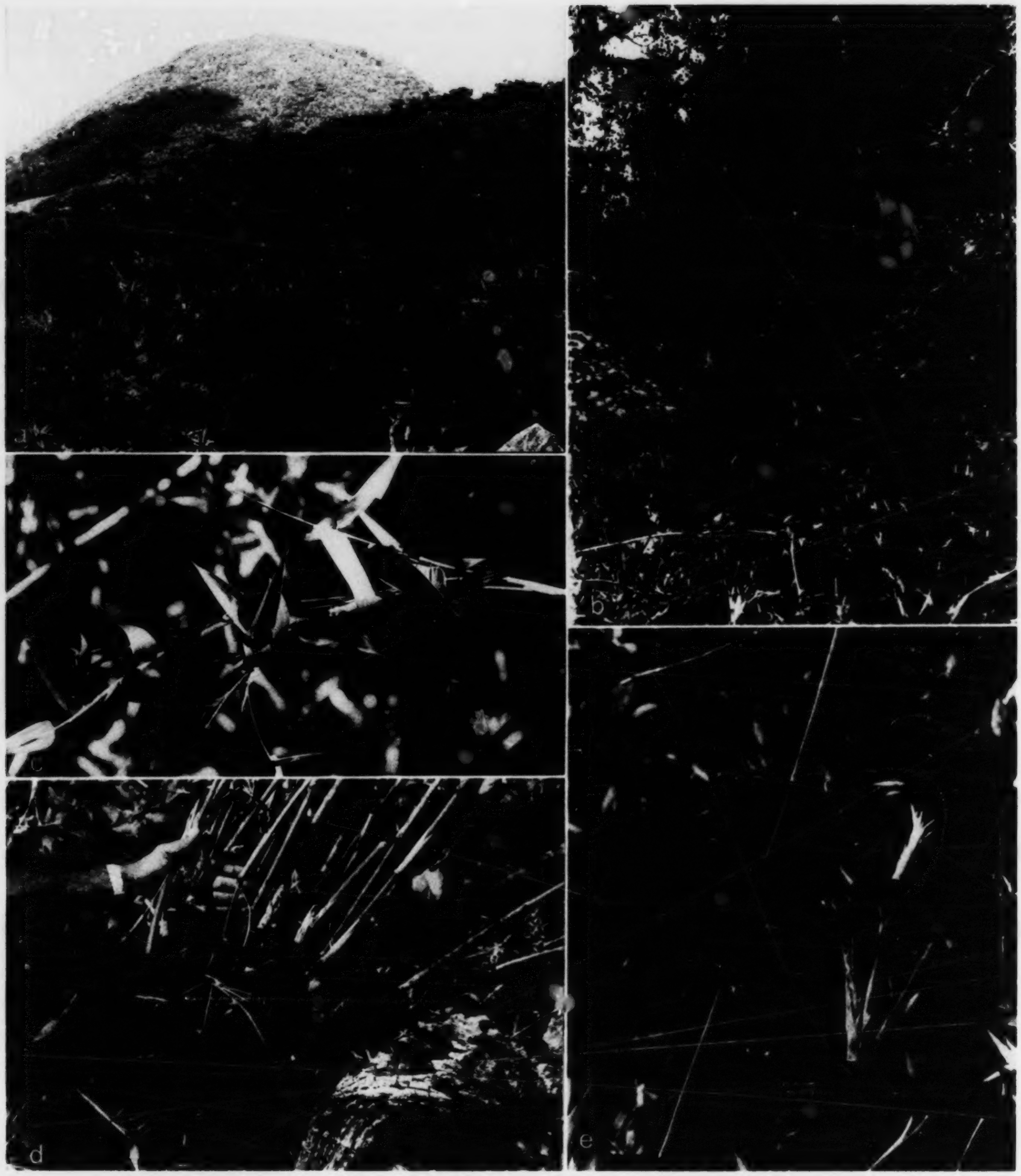

FIGURE 14.—Field photographs of *Arundinaria scandens* Soderstrom & Ellis, new species, in shrubby vegetation (e.g., *Rhododendron arboreum*) near the summit of Pidurutalagala (2500 m): *a*, habit; *b*, scandent culms, these becoming thick toward the summit; *c*, branches with thick foliage; *d*, base of an uprooted clump; *e*, new culm showing culm leaf with small reflexed blade and in background new clusters of branches. (All photographs show *Soderstrom & Kulatunge 1608*.)

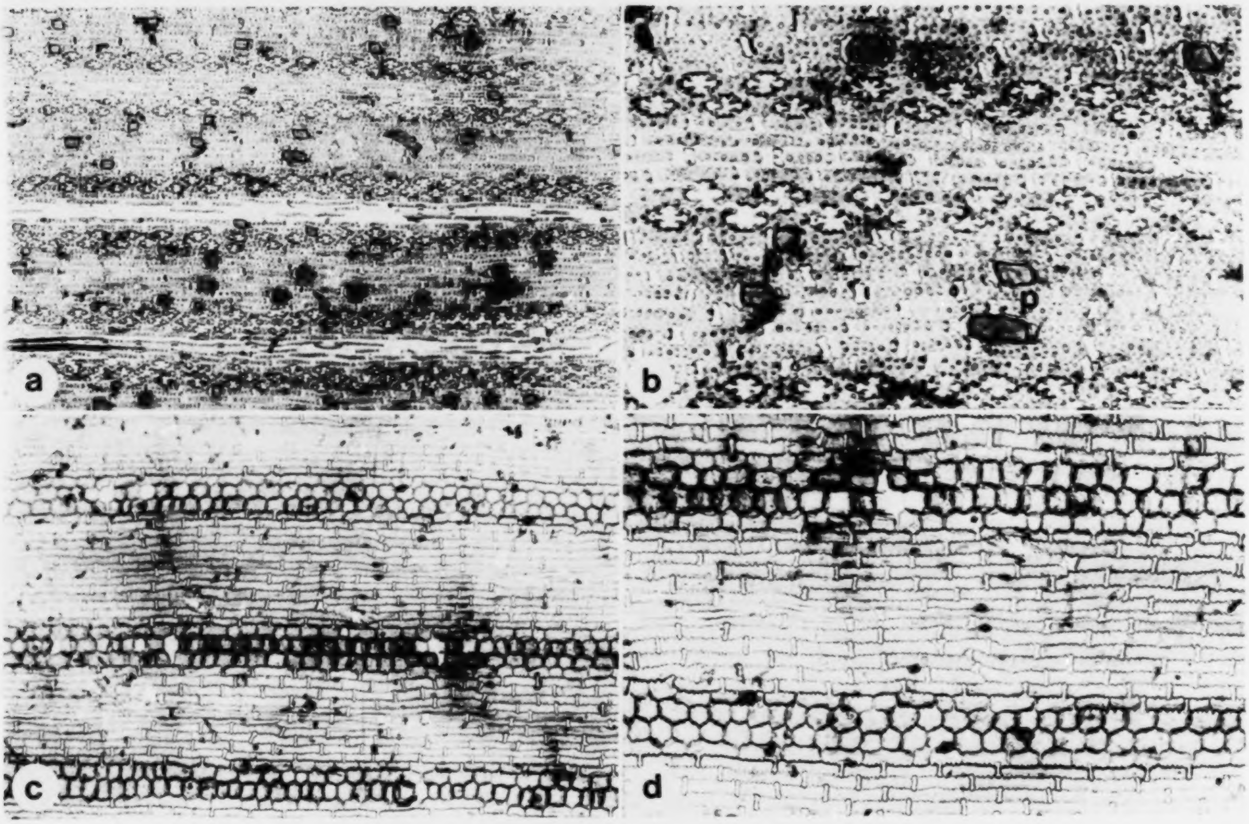

FIGURE 15.—Epidermal structure of *Arundinaria scandens* Soderstrom & Ellis, new species: *a*, abaxial epidermis showing costal and intercostal zones (×88); *b*, abaxial epidermal detail of papillae, prickles (p), microhairs and silica bodies (×220); *c*, adaxial epidermis with bulliform cells in center of intercostal zones and costal zone cell structure identical to that of the lateral intercostal files (×88); *d*, bulliform cell shape and arrangement and costal and intercostal long and short cells (×138). (Based on *Soderstrom 2551*.)

1608 (PDA, US), *Soderstrom 2551* (B, CANB, DD, K, LE, P, PDA, PRE, TNS, US); *Clayton 5756* (PDA, US).

DISCUSSION.—The Peradeniya sheet of the type of *A. scandens* bears several annotations, among them "*Arundinaria walkeriana* Munro" and "*A. wightiana* var. vel aff." Beddome (1873) himself wrote "certainly not *Arundinaria wightiana* of S. India." Munro had cited (1868), under the original description of *Arundinaria walkeriana*, specimens collected by Thwaites (*C. P. 3860*) from the same summit, but Gamble (1896) cited it under *A. wightiana* in his treatment. *Arundinaria wightiana* Nees von Esenbeck is a species from the Nilgiri Hills in southern India, with tall erect culms, while this new Sri Lanka species has rampant and clambering culms that are erect only during their early growth. The blades of *A. wightiana* are green on both surfaces, while those of the new species are green above and bluish green below.

This new species replaces *A. debilis* on Mount Pidurutalagala at elevations above 2100 meters.

ANATOMY

FIGURE 15

DESCRIPTION.—*Leaf blade in transverse section:* No preserved anatomical material was available for this study.

Abaxial epidermis. Intercostal long cells: elongated with parallel side walls and vertical end walls; walls unthickened, sinuous; cell shape constant across intercostal zones; no bulliform cells; short cell pairs or stomata present between successive long cells. *Stomata:* low dome-shaped but shape obscured by overarching papillae; 2–3 files of stomata adjacent to the costal zones; one interstomatal cell between successive stomata. *Intercostal short cells:* paired or single; silica cell very small, tall and narrow, often absent; cork cell square in shape with a crenate outline (Figure 15*b*); present between all long cells in central files of intercostal zones. *Papillae:* small, thickened, cuticular; present on all long cells including those of the costal zones (Figure 15*b*); up to 10 papillae in single row on each long cell of central intercostal files; interstomatal files with irregular arrangement but often with two rows of papillae; 4–6 papillae overarch stomata. *Prickles and hooks:* central intercostal files with large elongated barbless asperities (Figure 15*a,b*). *Microhairs:* rather short, only twice length of stomata; distal cell deciduous; basal cell appears to be silicified (Figure 15*b*); present between the stomatal zones and the central intercostal files. *Macrohairs:* absent. *Silica bodies:* tall and narrow, vertically orientated; same width as costal long cells; closely associated with cork cell (Figure 15*b*); intercostal silica bodies very small, of irregular occurrence, enfolded by cork cells. *Costal cells:* long cells very similar in length and width to the central intercostal long cells; alternate with cork-silica cell pairs along costal cell files; costal zones from 4–6 cells wide.

Adaxial epidermis. Intercostal long cells: elongate rectangular with slightly sinuous walls (Figure 15*d*); separated by single short cells; costal and lateral intercostal files of identical cells; central four intercostal files consist of bulliform cells; short, hexagonal in shape with middle two files alternating and interlocking (Figure 15*d*). *Stomata:* absent. *Intercostal short cells:* single, tall and narrow short cell positioned between all long cells except the bulliform cells. *Papillae:* absent. *Prickles and hooks:* absent. *Microhairs:* absent. *Macrohairs:* absent. *Silica bodies:* tall and narrow; short cells may rarely be silicified; costal and intercostal silica bodies identical. *Costal zones:* indistinguishable in cell structure from intercostal zones in surface view.

SPECIMEN EXAMINED.—*Soderstrom 2551*, Sri Lanka.

DISCUSSION.—In marked contrast to *Arundinaria floribunda*, small, cuticular, non-refractive papillae are present in this species, and the microhairs are short, only twice the length of the stomatal complexes.

5. *Arundinaria walkeriana* Munro

Arundinaria walkeriana Munro, 1868:21 [type: *Mrs. Walker 96 or 1304*, lectotype, *Walker 96*, K, not seen].—Beddome, 1873:230.—Gamble, 1896:3–4, pl. 1.—Hooker f. in Trimen, 1900:309.

Arundinaria wightiana sensu Thwaites, 1864:444 [not sensu Nees von Esenbeck, 1835:483].

Indocalamus walkerianus (Munro) Nakai, 1925:149.—Alston, 1931:342.—Senaratna, 1956:29–30, pl. 1.

MORPHOLOGY

FIGURES 16, 17

DESCRIPTION.—Shrubby bamboo of densely placed culms from sympodial, pachymorph rhizomes, with hollow culms to ~2 m (?) tall, the internodes smooth, when young lime green to maroon or a combination of both, becoming dull green at maturity. *Culm leaves* deciduous: sheath light green becoming stramineous, strongly ribbed, ciliate along the overlapping margin, on the back glabrous above, sparsely papillose below and at the base densely hirsute, this remaining as a hairy ring after the sheath falls, upper margins of sheath on either side of the ligule with erect white silky hairs 3–5 mm long; blade 2–3 cm long, $^1/_2$ cm wide, about $^1/_3$ the length of the sheath, narrowly ovate with a truncate base and acute tip, positioned more or less horizontally or slightly reflexed; ligule membranous, less than 1 mm long, pilose on the back. *Nodes* containing a single branch bud. *Branching:* central branch and two lateral branches developing more or less simultaneously, quickly followed by development of basal buds to produce a complement of up to 30 branches, these rarely rebranching, but continuing in length to ~40 cm, with 10–20 leaves, with production of new leaves and shedding of old blades, the old branches ultimately naked at the base, consisting of only hard, persistent, overlapping sheaths. *Foliage leaves* glabrous, blades terminal to the culm up to 15 cm long and 5 cm wide, those on the branches to 10 cm long and 2 cm wide, thick and leathery, more or less cordate-clasping at the base, the broad basal margins sometimes overlapping, the blades broadly lanceolate, narrowed to an acute navicular hard brown pointed tip, the midvein prominent, the margins cartilaginous and antrorsely scabrous, transverse veinlets prominent on both surfaces, the blades abscissile with age; sheath summit with white silky hairs on either side of the petiole, 3–4 mm long; ligule a membrane ~0.2 mm long with cilia ~1.5 mm long; petiole thick, 2–2.5 mm long. *Inflorescence* terminating the culm a large spreading panicle 20–30 cm long and about as broad, smaller on the branches, the branches glabrous and with pulvini on the upper surfaces at the axils, the pedicels up to 17 mm long, each bearing a many-flowered spikelet. *Spikelets* purplish, 14–20 mm long, usually 4- or 5-flowered, the lowest floret longest and most complete, the uppermost smallest and aborted, each separated by a narrow rachilla segment flat and glabrous below, dilated upward and white-pubescent on the expanded portion, the hairs dense on the rim at its juncture with the anthecium. *Glumes* 2, variable in length, the lower shorter than the upper, spreading out at maturity and becoming dried and thinner on the upper part, tearing or breaking off; glume 1 a little shorter than glume 2, the latter ~$^1/_3$–$^4/_5$ as long as the lemma; 1st glume 5.8 mm long, ovate-lanceolate, 7-nerved with a couple of transverse veinlets, glabrous on the back, ciliate on the margins; 2nd glume 6.5 mm long, the same shape as the first but longer, 7-nerved, ciliate on the upper margin. *Lemma* of lowermost floret ~7.3 mm long, ovate with an acute-apiculate apex, 9-nerved, ciliate on the upper margins; *palea* a little shorter than the lemma, thin, with 2 keels and broad wings, each 2-nerved, mucronate at the apex, appressed puberulent on the upper part between the keels and ciliate at the apex; *lodicules* 3, ~1.4 mm long, diaphanous, lanceolate, many-nerved, ciliate on the upper margins; *andrecium:* stamens 3, the anthers orange, ~5 mm long; *gynecium:* ovary with 3 (2) plumose stigmas. *Fruit* an elliptic caryopsis ~5 mm long with a short beak (the persistent base of the style), the embryo basal, ~$^1/_5$ the length of the fruit, the hilum linear, extending the entire length of the caryopsis in a furrow on the

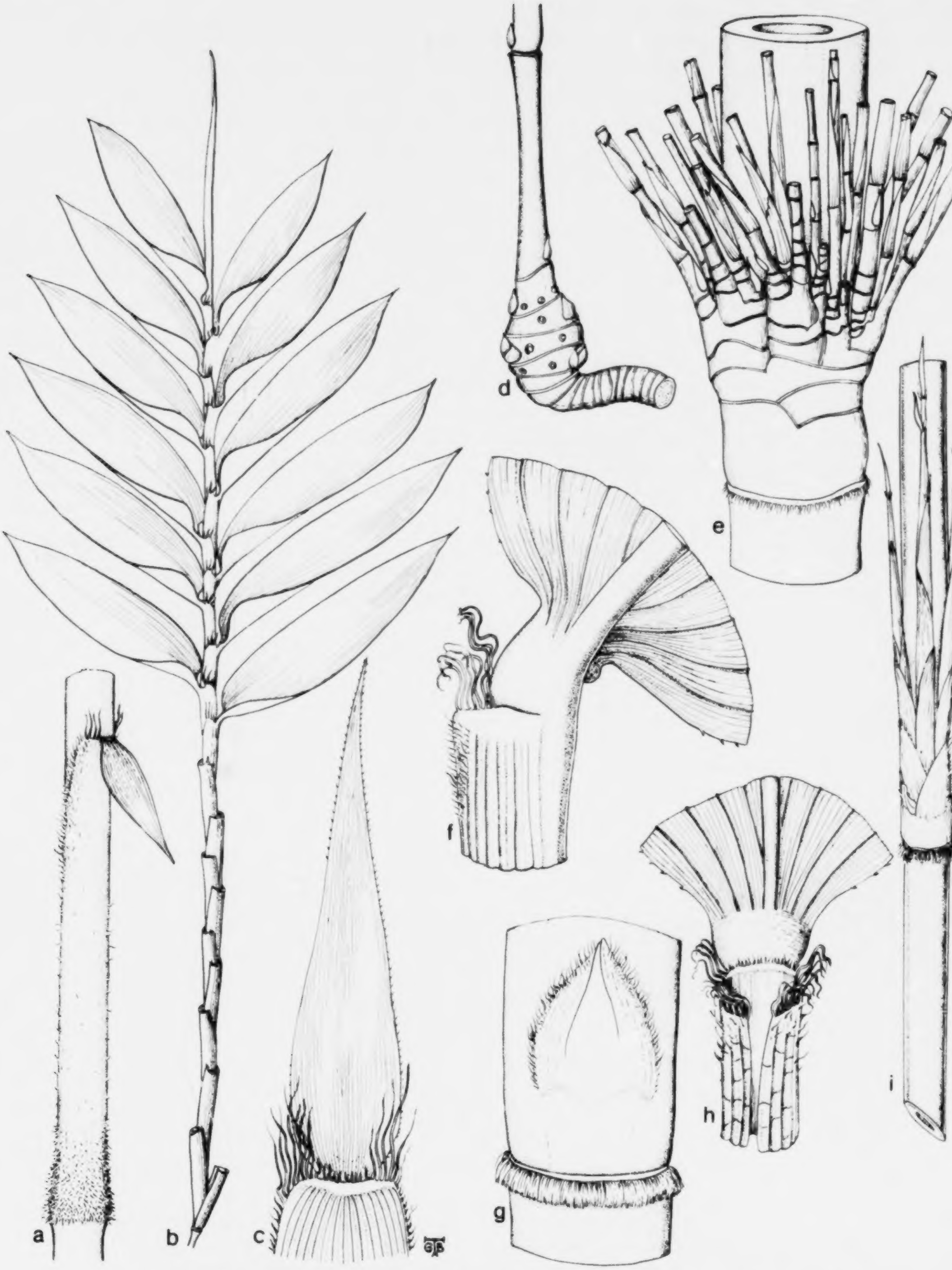

FIGURE 16.—*Arundinaria walkeriana: a*, culm sheath in place (×1.2); *b*, leaf complement (×0.6); *c*, culm sheath (adaxial view) (×1.7); *d*, rhizome bud pattern (×1.2); *e*, mature branch complement (×3); *f*, leaf ligule, side view (×7); *g*, bud on new culm (×3); *h*, leaf ligule, front view (×6); *i*, young branch complement (×1.2). (All illustrations by G.B. Threlkeld, based on *Soderstrom & Kulatunge 1772*.)

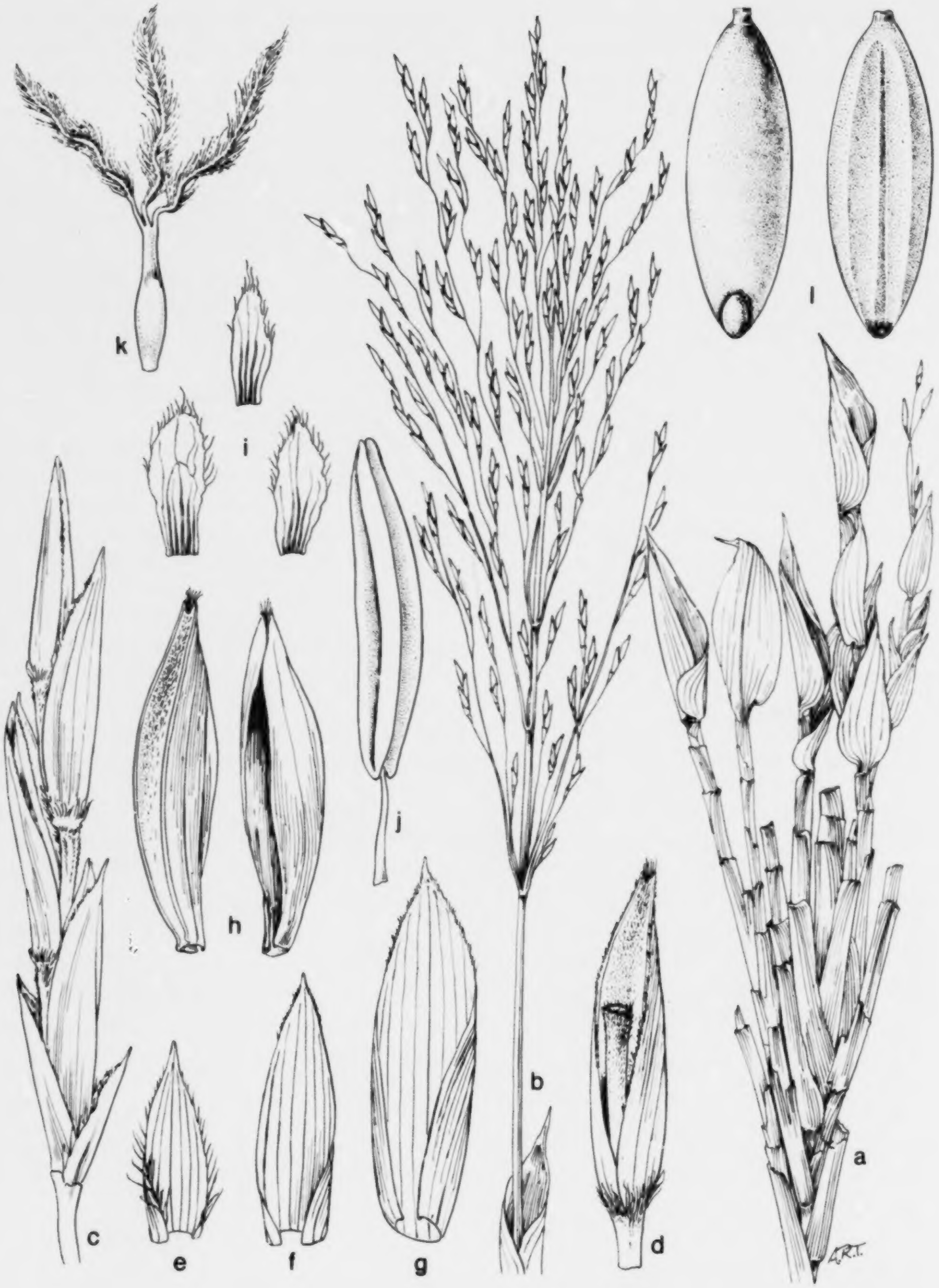

FIGURE 17.—*Arundinaria walkeriana*: *a*, vegetative branches (×0.6); *b*, new inflorescence recently emerged from subtending sheath (×0.6); *c*, spikelet (×7); *d*, floret (×11); *e*, glume I (×11); *f*, glume II (×11); *g*, lemma (× 11); *h*, palea, side view showing keels and frontal view (×11); *i*, lodicules, lower anterior pair and upper posterior (×15); *j*, anther (×15); *k*, gynecium (×15); *l*, caryopsis, embryo view and hilum view (×11). (*a*, *b*, and *l* based on *Ferguson s.n.* in 1887, Knuckles Mountains; all others based on specimens from Dumbanagala, Rangala, 28 Sep 1888, *s. coll.*)

convex side.

DISTRIBUTION.—Apparently endemic to the upper montane zone of the Central Province. Gamble (1896:4) also listed the species as occurring in the Pulney [Palni] Hills of southern India, on the basis of a collection made there in 1873 by Beddome. But Gamble does go on to remark that in Beddome's specimens, which consisted of leaves only, the leaves were larger and narrower than those from Sri Lanka gatherings. The Palni species is indeed a much larger one and distinct in many ways, and appears to be undescribed.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—BADULLA DISTRICT: Wattakelle Hill, *Ferguson s.n.* (PDA, mounted on sheet marked *C. P. 429*, Wattakelle Hill, 1879); Wattekelle Hill, 1879, *C. P. 429* (PDA); Wattekelle Hill, 1879, *C. P. 429* (PDA, mounted on sheet with flowering fragment marked "Wattakelle Hill, 1869, W. F."); Knuckles and Wattekelle, 1866, *C. P. 429* (PDA). KANDY DISTRICT: Knuckles Mountains, Mar 1887, *Ferguson 312* (PDA); Knuckles Mountains, 1800 m alt., *Gould & Balakrishnan 13897* (PDA, US); Dumbanagala, Rangala, ~5000 ft. [~1520 m] alt., Sep 1888, *s. coll.* (PDA); Dumbanagala, Rangala, 28 Sep 1888, *s. coll.* (PDA). NUWARA ELIYA DISTRICT: Adam's Peak, *Gardner s.n.* (PDA, mounted on sheet with other specimens marked *C. P. 429* and Wattekelle 1885, Knuckles 1886); on the way to Adam's Peak from Halton side, near Edikatupane, 2330 m alt., *Soderstrom & Kulatunge 1772* (US).

DISCUSSION.—We have chosen *Walker 96* as the lectotype for this species as it is the first one listed by Munro in the original description and this plus *Walker 1304* were the basis of the illustration given by Gamble. *Thwaites 3860* consists of flowering specimens from Pidurutalagala, and is listed with the original description of the species, but this collection pertains to the new species here described as *Arundinaria scandens*. While Gamble (1896:5) recognized Munro's error, he himself assigned the Thwaites collection to *Arundinaria wightiana*, but we have shown elsewhere that that species is confined to the Nilgiri Hills of southern India.

The illustration of this species in Senaratna (1956, pl.1) is apparently of a small flowering offshoot of a larger plant and is not at all representative of the species. Trimen (1900) gives southern India ("Pulney Hills") as a locality for the species, erroneously following Gamble, who had placed Beddome's collection of 1873 there; the Palni species is undescribed. The species that Trimen mentions as being in profuse bloom on the summit of Pidurutalagula in 1884 is *Arundinaria scandens*.

ANATOMY

FIGURE 18

DESCRIPTION.—*Leaf blade in transverse section:* No preserved leaf blade material was available for anatomical study.

Abaxial epidermis. Intercostal long cells: rectangular; detail obscured by papillae (Figure 18*b*); no bulliform cells. *Stomata:* shape indistinguishable due to overlapping papillae; three files of stomata appear to be present on either side of each costal zone; one interstomatal cell present between successive stomata in a file. *Intercostal short cells:* single with crenate outlines (Figure 18*b*); detail often obscured by papillae. *Papillae:* conspicuous, very plentiful, darkly staining; present on all long cells (Figure 18*a,b*); pattern of arrangement not regular but central files tend to have a double row with up to 14 papillae per long cell (Figure 18*b*); laterally situated papillae often not vertical but inclined, overlapping stomata and adjacent long cells. *Prickles and hooks:* identical costal and intercostal prickles dominate this surface (Figure 18*a,b*); bases elliptical, associated with short cells and barbs well developed and point in all directons; absent only from stomatal files. *Microhairs:* narrow rod-like (Figure 18*b*); common in intercostal zones but often obscured by papillae. *Macrohairs:* absent. *Silica bodies:* tall, saddle-shaped but obscured by papillae and prickles; few present on costal zones where prickles appear to replace them; apparently absent form the intercostal zones. *Costal cells:* costal zones distinct (Figure 18*a*) consisting of 2–3 files of cells; due to numerous prickles no silica body pattern of arrangement is evident.

Adaxial epidermis. Intercostal long cells: elongated, rectangular with slightly sinuous walls (Figure 18*c,d*); length up to 7× greater than width; separated by single or paired short cells; costal and lateral intercostal files of identical cells but costal zones recognizeable due to underlying fibers (Figure 18*b*); central four files of long cells in each intercostal zone consist of bulliform cells (Figure 18*c,d*); the middle two files of each bulliform file with short, hexagonal cells with thickened walls (Figure 18*d*) and may be silicified (Figure 18*c*). *Stomata:* absent. *Intercostal short cells:* single or paired (Figure 18*d*); cork and silica cells tall and narrow but silica cell much smaller than cork cell; present between all long cells except bulliform cells. *Papillae:* absent. *Prickles and hooks:* absent. *Microhairs:* absent. *Silica bodies:* small, tall and narrow to crescent-shaped (Figure 18*d*); irregular in occurrence in intercostal zones; present between all costal long cells but these very elongated. *Costal zones:* narrow, consisting of only one or two cell rows; long cells elongated, of same size and shape as intercostal long cells; alternate with cork-silica cell pairs.

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1772*, Sri Lanka.

DISCUSSION.—No leaf transverse sections were examined but the epidermal structure conforms closely to that characteristic of the Arundinariinae. The numerous, conspicuous, strongly barbed abaxial prickles are of interest as is the absence of adaxial prickles.

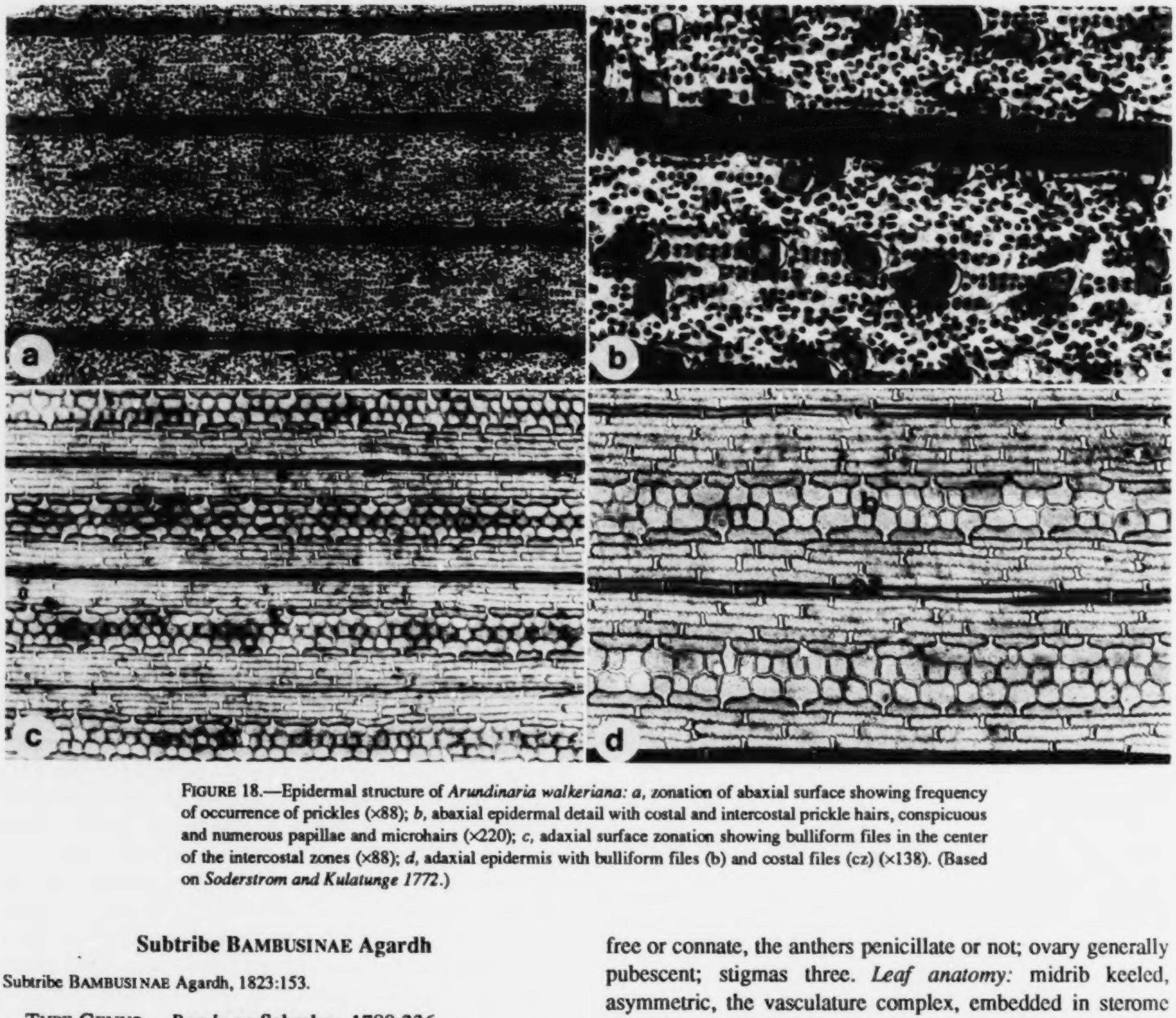

FIGURE 18.—Epidermal structure of *Arundinaria walkeriana: a,* zonation of abaxial surface showing frequency of occurrence of prickles (×88); *b,* abaxial epidermal detail with costal and intercostal prickle hairs, conspicuous and numerous papillae and microhairs (×220); *c,* adaxial surface zonation showing bulliform files in the center of the intercostal zones (×88); *d,* adaxial epidermis with bulliform files (b) and costal files (cz) (×138). (Based on *Soderstrom and Kulatunge 1772.*)

Subtribe BAMBUSINAE Agardh

Subtribe BAMBUSINAE Agardh, 1823:153.

TYPE GENUS.—*Bambusa* Schreber, 1789:236.

DIAGNOSIS.—*Morphology:* Plants erect or vining, loosely to densely cespitose; rhizomes sympodial; culms hollow to solid, armed or unarmed; primary branch buds solitary at midculm nodes, the branching usually intravaginal; inflorescences iterauctant; pseudospikelets present, 2–many-flowered, the uppermost floret reduced; stamens usually 6, the filaments free or connate, the anthers penicillate or not; ovary generally pubescent; stigmas three. *Leaf anatomy:* midrib keeled, asymmetric, the vasculature complex, embedded in sterome tissue; arm cells and fusoid cells well developed; fan-shaped clusters of bulliform cells prominent; silica bodies vertically oriented, saddle-shaped; papillae cuticular, often bifurcating, overarching the stomates.

DISTRIBUTION.—As defined by Soderstrom and Ellis (1987), a subtribe of 7 genera confined to the tropics of Africa, Asia, and northern Australia, usually in wet, lowland sites.

Key to the Genera of the Bambusinae in Sri Lanka

1. Stamen tube absent; lodicules 3; pseudospikelets with all florets disarticulating between the rachilla segments; plants introduced, cultivated, 2 of the 3 species more than 10 m tall and 10 cm in diameter . . . . *Bambusa*

1. Stamen tube present; lodicules absent; pseudospikelets with florets not disarticulating except below the lowest lemma; native plants less than 10 m tall and 10 cm in diameter.

2. Culms stout, erect; branching intravaginal; midculm nodes with primary branch buds not exhibiting dormancy, the primary branches stout, not whip-like; pseudospikelets few (~10–20), in a hemispherical fascicle; culm leaves with prominent oral setae and inconspicuous sheath auricles; stigma 1; anthers not penicillate . . . . **Dendrocalamus**
2. Culms weak, the plants vine-like; branching extravaginal; midculm nodes with primary branch exhibiting a period of dormancy, with subsidiary branches developing precociously, the primary branch whip-like; pseudospikelets many (~100) in a spherical cluster; culm leaves with oral setae very short and prominent sheath auricles; anthers penicillate; stigmas 3 . . . . **Pseudoxytenanthera** Soderstrom & Ellis, new genus

Genus *Bambusa* Schreber, 1789, nom. cons.

Bambusa Schreber, 1789:236.

TYPE SPECIES.—*Bambusa bambos* (Linnaeus) Voss, 1896:1189.

DIAGNOSIS.—*Rhizomes* sympodial, pachymorph, rarely with elongated necks. *Culms* usually in dense, cespitose clumps, typically self-supporting, rarely weak and not self-supporting or scandent; internodes terete or shallowly sulcate above the locus of emergence of buds or branches, hollow, rarely solid; nodes flat or with an upper ridge and biannular; branch buds broad, positioned at the nodal line, sometimes lacking at the base, or in the middle, or from the base to the middle of the culm, the buds (generally at lower culm nodes) in some species producing secondary branches from lateral primordia while major primordium remains dormant within the prophyllum. *Branching* intravaginal, extravaginal sometimes also occurring in some branches of the same plant. *Branch complements* at midculm nodes positioned at or very near the nodal line, with the primary axis dominant and subdominant secondary axes produced from its base, the production of progressively smaller branches from the swollen base of successively higher orders often continuing over several years to form a more or less strongly congested tuft of unequal branches, the larger ones usually rebranching at their upper nodes, the smaller ones not; in a few species the midculm branch complements showing all of the branches unequal, or the median one only slightly or not at all dominant. *Culm leaves* quite variable, caducous or persistent, the blade erect or reflexed. *Leaf-blades* petiolate, with transverse veinlets usually not manifest externally, when manifest typically distant, nodular, translucent in transmitted light. *Pseudospikelets* solitary or, more commonly, forming fascicles, tufts, or dense capitate clusters, the lowest bracts (above the prophyllum) all subtending buds or some not, the next higher ones (where the spikelet begins) subtending sterile or fertile florets. *Spikelets* terminating in a perfect floret, a depauperate floret, or in a slender prolongation of the rachilla, this commonly bearing a minute rudiment or a depauperate floret; transitional glumes 1–several; functional florets 1–many, hermaphrodite, rarely staminate with the pistil obsolete (probably only in old and depauperate inflorescences where spikelets in this condition are referred to as polygamous), loosely to rigidly inflated to more or less strongly compressed; lemma fully embracing the palea only basally or tightly amplectant throughout; palea usually gaping, convex or faintly to markedly sulcate and keeled dorsally, entire or emarginate or deeply cleft apically; rachilla segments elongated and disarticulating below the lemma of fertile florets or short and not disarticulating, the spikelet falling entire; lodicules 3, 2, or 0 (usually when the filaments are united), unequal and unalike, the anterior asymmetric and paired, sometimes connate, the posterior symmetrical and narrower, all thin throughout or the anterior ones turgid at anthesis; stamens typically 6, the anthers apically emarginate, mucronate or penicillate, the filaments filiform and free or flattened and more or less connate and forming a delicate tube; ovary solid, thickened at the top where generally pubescent; style short or long, branched or unbranched; stigmas 3, 2, or 1, plumose. *Fruit* a caryopsis, ovate to oblong, beaked, with the base of the style and upper part of the pericarp markedly thickened and indurated at the apex and more or less downward, thinner toward the base with correlated manifestation or obscurity of the hilum and embryotegium.

DISTRIBUTION.—Several dozen species of tropical southern and eastern Asia.

Key to the Species of *Bambusa* in Sri Lanka

1. Plants armed, the lower branches spiny; plants tree-like, the culms often greater than 10 m tall and 10 cm in diameter . . . . 6. ***Bambusa bambos***
1. Plants unarmed, tree-like or shrubby.
   2. Auricles of culm sheath present, prominent; plants large, tree-like, usually greater than 10 m tall and 10 cm in diameter; undersurface of leaves green . . . . 8. ***Bambusa vulgaris***

2. Auricles of culm sheath absent; plants shrubby, less than 5 m tall and 5 cm in and
5 cm in diameter; undersurface of leaves bluish green . . . .
. . . . 7. ***Bambusa multiplex***

6. *Bambusa bambos* (Linnaeus) Voss

Bambusa bambos (Linnaeus) Voss, 1896:1189.

Arundo bambos Linnaeus, 1753:81.

Bambusa spinosa Roxburgh, 1814:25.—Munro, 1868:104–105.—Beddome, 1873:231–232.

Bambusa [as *Bambos*] *arundinacea* Retzius sensu J.A. and J.H. Schultes in Roemer and Schultes, 1830:1340–1342.—Beddome, 1873:231.—Gamble, 1896:51–55, pl. 48.—Gamble in Hooker, 1896:395–396.—Hooker f. in Trimen, 1900:313–314.—Camus, 1913:128–129, pl. 74: fig. A, and pl. 75: fig. A.

Bambusa orientalis Nees von Esenbeck, 1835:472 [nomen nudum].—Munro, 1868:105–106.—Beddome, 1873:231.—Senaratna, 1956:27.

MORPHOLOGY

FIGURES 19–21

DESCRIPTION.—Plants of unicespitose habit from sympodial, pachymorph rhizomes, producing large dense clumps of closely placed culms. *Culms* strong, cylindrical, hollow, erect, up to 30 m tall, 5–10 cm diam., the walls very thick with a small lumen or almost solid on the upper part of the culm or distal parts of branches, branching at all the nodes, those from the lower nodes recurved and bending downward to the ground, the upper branches horizontal or ascending and producing a gently arching fan-like plume, the lower entangled branches spine-like, the upper leafy branches bearing small spines, new and old culms dark green, glabrous. *Culm leaves* dark maroon when young, becoming stramineous and with maroon striping, appressed, succulent and leathery, pushed off by the emerging branches and becoming caught among the entangled mass of branches; sheath wrinkled at the summit, glabrous except for a dense ring of hairs at the base, ciliate on the upper margins, gradually merged into the blade; blade erect, persistent, much shorter than the sheath, triangular above with a broad sloping and wrinkled base on either side, glabrous on the outside except for the brown, pilose wrinkled portion, densely covered on the inside by dark brown appressed hairs, producing a felt-like appearance; inner ligule a tiny brown ciliate membrane; outer ligule lacking. *Nodes* containing a single branch bud at the prominently ridged nodal line. *Branching:* central dominant branch produced first with 1 or 2 laterals produced soon from its lower nodes, usually the primary and 1 secondary branch produced at the lower nodes of the culm, the branches recurved and bending downward, often spine-like, usually 3 branches produced at the upper nodes, leafy, with some branches spine-like. *Foliage leaves* diffuse, in complements 15–30 cm long, 8–15 cm wide, with 7–10 leaves in the complement; blades lanceolate, narrowed to an acuminate tip, 10–20 cm long, 1–2 cm wide, with an inconspicuous midvein on the upper surface and a prominent, stramineous elevated midvein on the lower surface, tessellation not manifest, glabrous; sheath somewhat compressed, glabrous except for the ciliate upper margins and flanks; inner ligule a tiny, inconspicuous, membranous ciliolate rim, puberulent abaxially; outer ligule a tiny, hard, glabrous ridge. *Inflorescences* at first terminating leafy branches, ultimately resulting in small clusters at the nodes of leafless branches. *Pseudospikelets* sessile, the subtending bract caducous, 15–17 mm long, narrowly obovate, stramineous, with 6–8 florets, successively longer upwards, the lower fertile, the upper 3 aborted and reduced; prophyllum 2-keeled, ciliate on the keels, 5 mm long, subtending a bud; gemmiferous bract 1, obovate-triangular, apiculate, 13-nerved, 6.8–7.7 mm long followed by the lemma of the spikelet proper; branching determinate, with the buds subtended by the prophyllum and bract developing into pseudospikelets upon maturity of the spikelet; disarticulation below the fertile lemmas, the florets falling separately. *Spikelets* consisting of several fertile florets, without empty glumes, the lowermost developing first and with reduction upwards; *lemma* broadly obovate-triangular, 17–19-nerved with transverse veinlets, short-ciliate on the margins, otherwise glabrous, apiculate, 8–11 mm long; *palea* elliptic, equal to or a little longer than the lemma, 2-keeled with long cilia on the upper $^2/_3$ of the keels, the keels broadly winged and enwrapping the flower, nerves with transverse veinlets, 6 between the keels, 4 in each wing; *lodicules* 3, the 2 anterior more or less obovate with a broad, slightly acute apex, ~1.8 mm long, glabrous except for the margins that bear long cilia ~$^1/_4$–$^1/_5$ as long as the body of the lodicule, the thin, many-nerved main portion appressed to the ovary, a thin forward flap of tissue appressed against the outer margin of the lower wing of the palea, the lodicule fleshy along the margin toward the center where the main body and forward flap of tissue are fused and contain many nerves, the posterior lodicule a single thin, many-nerved membrane, obovate with an acute apex, ~1.2 mm long, glabrous except for the ciliate upper margin; *andrecium–stamens* 6, the filaments long, filiform, free, anthers 4.7 mm long, basifixed, attached to the filaments on the lower $^1/_6$; *gynecium–ovary* glabrous below, hairy at the summit, with 3 stigmas arising from shortly above the summit, the style(s) variable in length and fusion; fruit a caryopsis, elliptic, glabrous except for a pubescent nipple at the summit, the hilum situated in a groove and extending almost the whole length of the caryopsis, embryo ~$^1/_5$ the length of the caryopsis, forming a discrete process at the base of it.

DISTRIBUTION.—Apparently native to southeastern Asia, and now widely introduced and cultivated throughout the tropics.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—ANU-

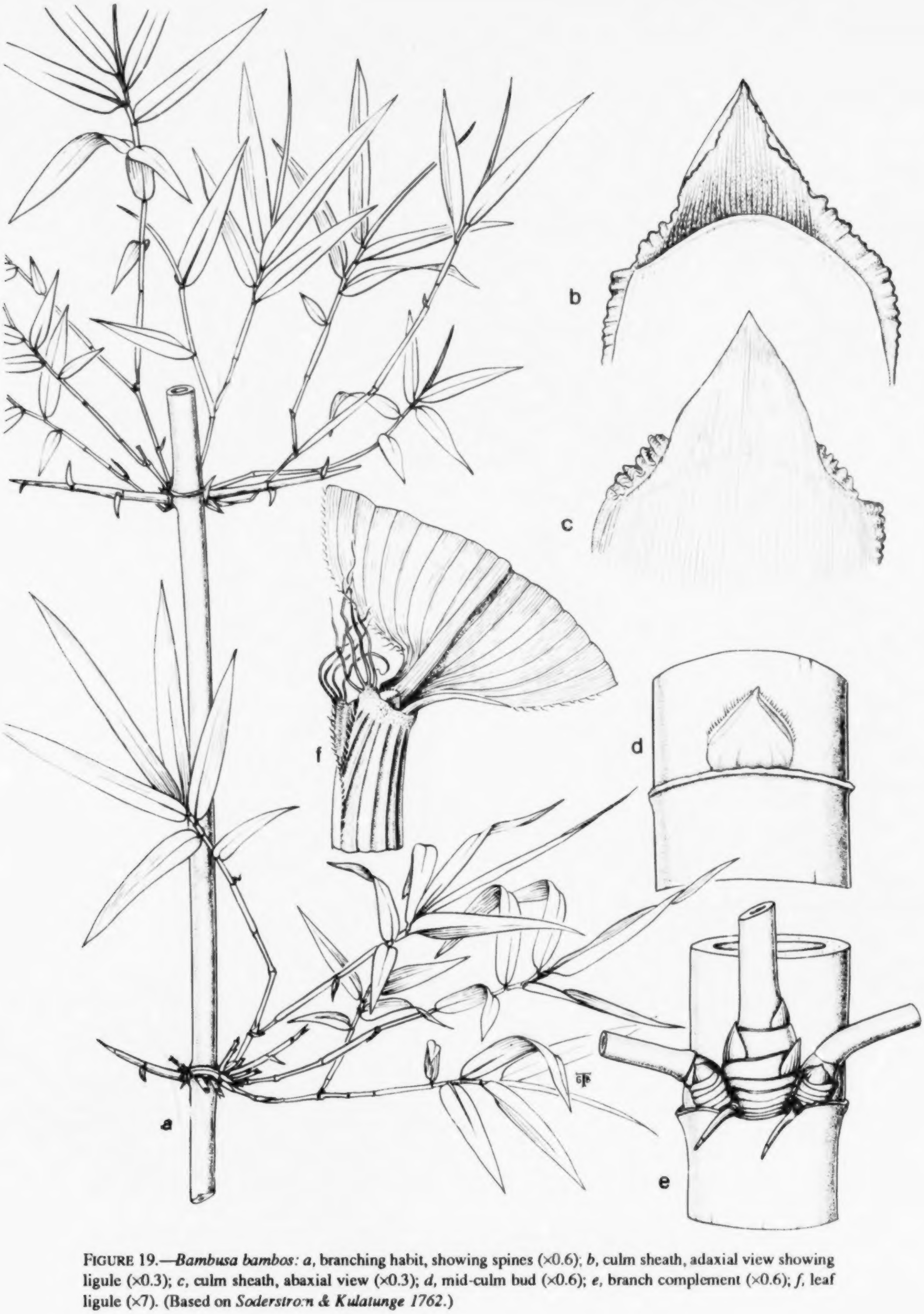

FIGURE 19.—*Bambusa bambos: a*, branching habit, showing spines (×0.6); *b*, culm sheath, adaxial view showing ligule (×0.3); *c*, culm sheath, abaxial view (×0.3); *d*, mid-culm bud (×0.6); *e*, branch complement (×0.6); *f*, leaf ligule (×7). (Based on *Soderstrom & Kulatunge 1762*.)

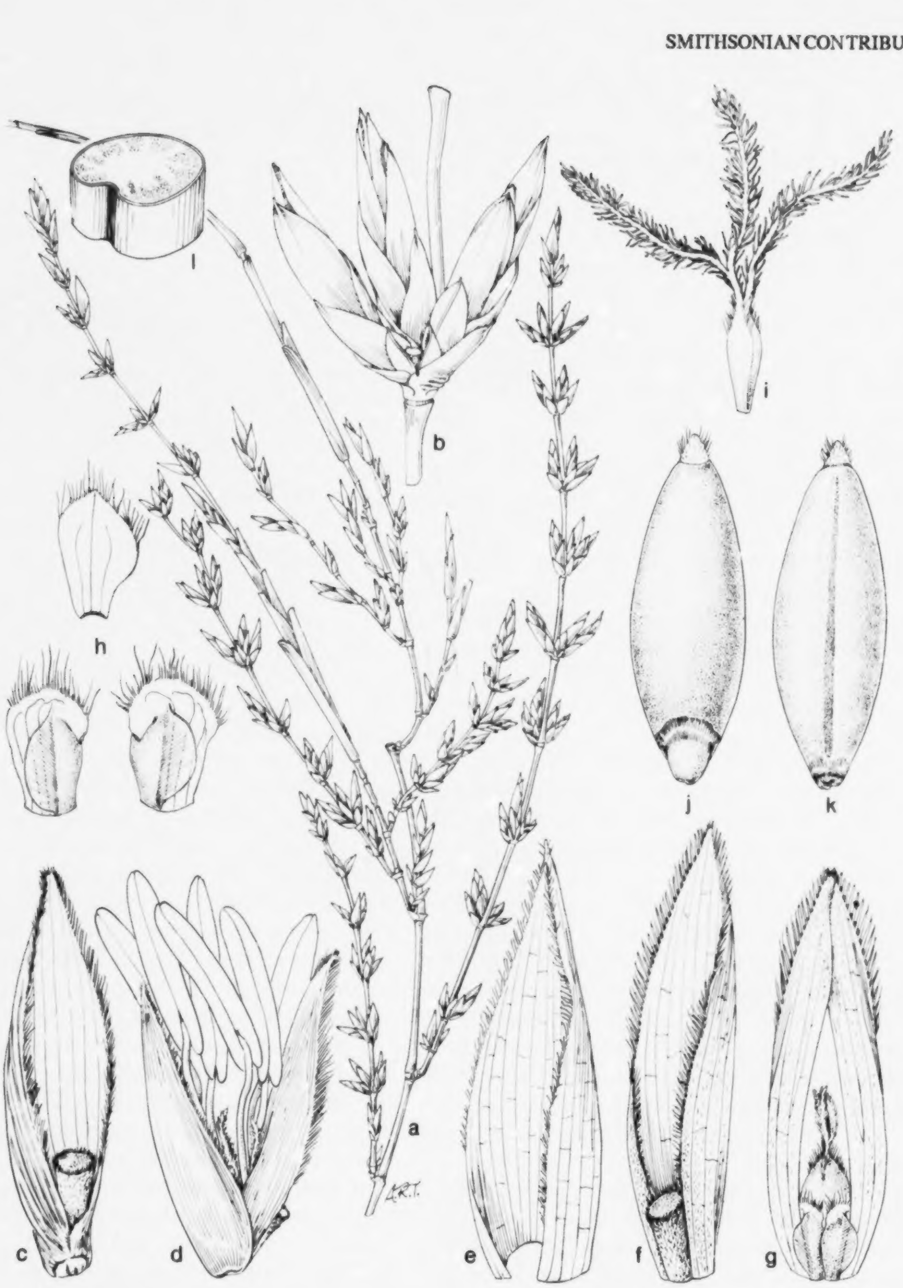

FIGURE 20.—*Bambusa bambos: a*, inflorescence branches (×0.5); *b*, cluster of young pseudospikelets, showing ciliate prophylla at the base of two of them (×3); *c*, floret (×6); *d*, lemma and palea of floret separated to show 6 stamens (×6); *e*, lemma (×9); *f*, palea, showing the strongly ciliate keels (×9); *g*, palea, from opposite side of *f*, showing overlapping margins above. Below, the position of the anterior lodicules shows the thin flaps of tissue covering the outside part of the lower palea margins while the remainder of the lodicule is inside the margins and lying against the ovary, which here is shown in a young stage (×9); *h*, lodicules, the posterior one above, the anterior two below. Note the thin flap of tissue in each of these extending away from the center (×13); *i*, gynecium (×9); *j*, embryo (dorsal) side of caryopsis (×6); *k*, hilum (ventral) side of caryopsis (×6); *l*, transverse section of caryopsis, showing hilum situated in the concave side (×9). (*a–c*, *e*, and *f* based on *C. P. 3320* from Sri Lanka; *d* and *g–i* on *Soderstrom 1998*, cultivated in Puerto Rico; and *j–l* on *Pohl and Lucas 13009*, cultivated in Costa Rica.)

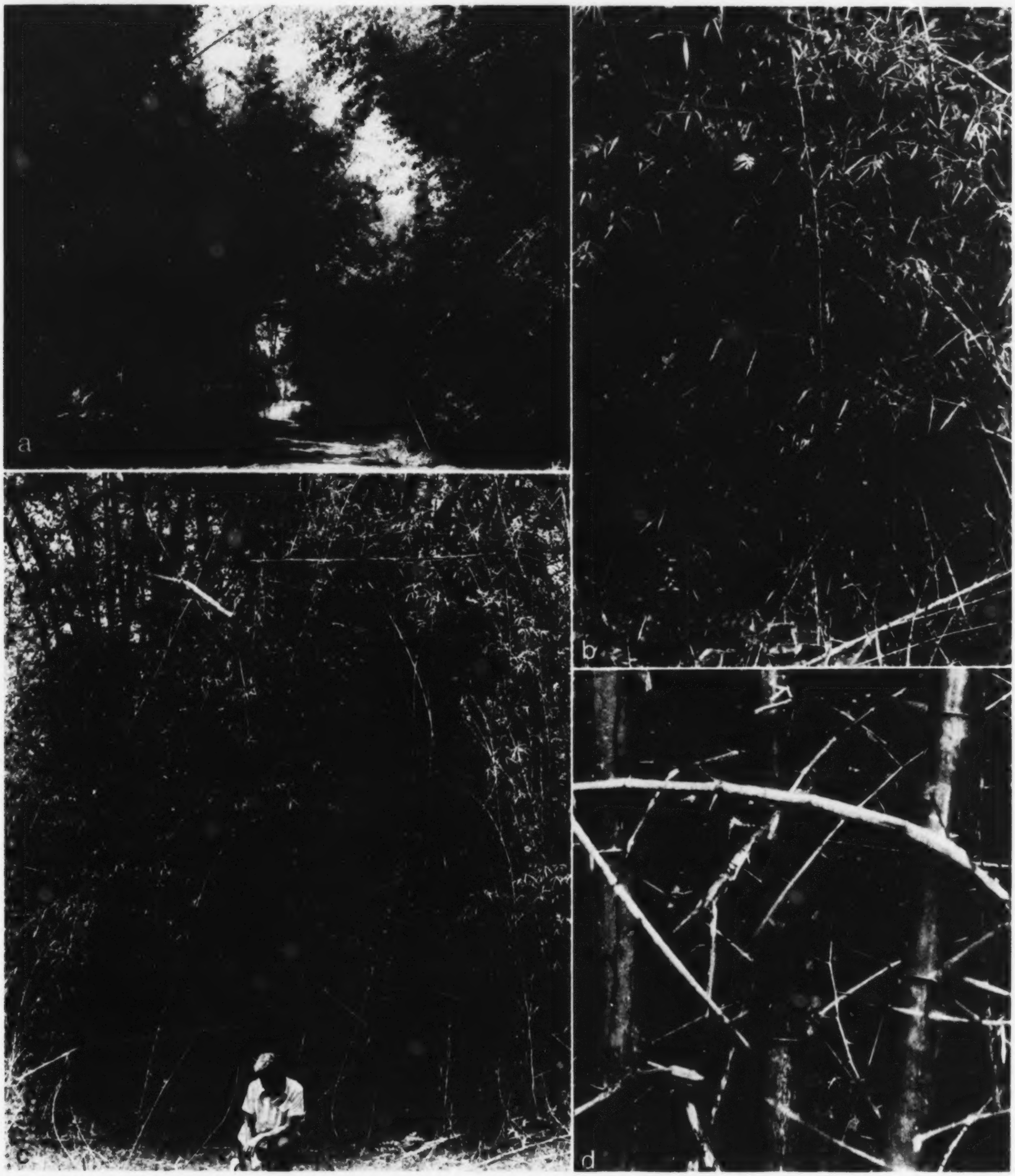

FIGURE 21.—Field photographs of *Bambusa bambos* along road at Sigiriya, Matale District (elev. ~120 m): *a*, full view of clumps; *b*, small, delicate foliage leaves; *c*, characteristic trailing culms and spiny branches from the lower nodes (G.B. Threldkeld, botanical illustrator, at base); *d*, intertwining spiny branches of lower nodes. (Photographs show *Soderstrom & Kulatunge 1762*.)

RADHAPURA DISTRICT: Ritigala Strict Natural Reserve, Unakanda, 1600 ft. [486 m] alt., *Jayasuriya 1099* (PDA, US). MATALE DISTRICT: Sigiriya, probably planted, *Soderstrom & Kulatunge 1762* (US). POLONNARUWA DISTRICT: "Alut Oya, Sep. 1885" written in ink on sheet but no label, *s. coll.* (PDA). KANDY DISTRICT: Peradeniya, Royal Botanic Gardens, cultivated, *Alston s.n.* (PDA). LOCALITY UNKNOWN: "Central Prov. 1855" written in pencil on sheet, *s. coll., C. P. 3320* (PDA).

DISCUSSION.—The nomenclature of this taxon is complex and is summarized by Soderstrom (1985); the synonymy given above is not complete. Details of the floret were taken from *Soderstrom 1998* (US vial no. 1228) as the small amount of Sri Lanka material at hand was old and in poor condition. The stigmas arise from the summit of the ovary directly or there may be a short style and branching from this.

ANATOMY

FIGURE 22

DESCRIPTION.—*Leaf blade in transverse section. Leaf outline:* expanded and flat; asymmetrical with the lamina on either side of the midrib being S-shaped (Figure 22*c*) and with the two margins differing somewhat in shape (Figure 22*a,b*); relatively thin (~75 µm thick). *Ribs and furrows:* absent, both surfaces flat (Figure 22*d*). Slight rib development associated with one margin only (Figure 22*b*). *Midrib:* consists of median vascular bundle only; larger than the lateral first order vascular bundles and associated with abaxial and adaxial sclerenchyma girders (Figure 22*c*); projects abaxially and with asymmetrical outline. *Vascular bundle arrangement:* 11 first order bundles in blade (including median vascular bundle); 6–9 third other vascular bundles located between consecutive first order vascular bundles; no second order bundles present (Figure 22*d*). All bundles located in the middle of the blade. *Vascular bundle description:* third order vascular bundles round to vertically elongated; first order vascular bundles round (Figure 22*d*); metaxylem vessels distinct with rounded lumens, unthickened; phloem adjoins the inner bundle sheath. *Vascular bundle sheaths:* double, even in third order bundles; round. Outer bundle sheath of first order vascular bundles with slight adaxial, but wider abaxial interruption; no bundle sheath extensions; outer bundle sheath cells irregularly elliptical, the lateral cells tending to be larger, thin-walled, inconspicuous with chloroplast-like contents. Inner sheath entire, single; cells with uniformly but heavily thickened walls (Figure 22*d*). *Sclerenchyma:* adaxial and abaxial girders associated with all vascular bundles; abaxial girders trapezoidal, narrowing towards the bundle; adaxial girders narrow and small. No sclerenchyma between the vascular bundles (Figure 22*d*). Small sclerenchyma cap at the margin; shape of left-hand and right-hand caps differs considerably (Figure 22*a,b*). *Chlorenchyma:* fusoid cell cavities absent particularly in lateral parts of leaf blade (Figure 22*a,b*); only irregularly present near the midrib (Figure 22*c*). Adaxial layer of chlorenchyma cells with conspicuous vertical invaginations from lower cell walls; remainder of arm cells with invaginations of equal length from all walls (Figure 22*d*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups conspicuous, raised, fan-shaped, occupy about one-half of the leaf thickness (Figure 22*d*); central cell of group large and shield-shaped and associated with only a single bulliform cell on either side; bulliform cell files, therefore, are only 3 cells wide; bulliform cells without thickened cuticle. Outer walls of remaining epidermal cells covered by a thick cuticle; costal and intercostal cells of similar size and shape. No papillae or hairs. *Abaxial epidermis:* no bulliform cells; each cell with individual thickened cuticle, often projected into thickened, cuticular papillae (Figure 22*d*); one papilla per cell as seen in transection; no macrohairs; very few prickles and hooks.

Abaxial epidermis (Figure 22*e*). *Intercostal long cells:* elongated, with parallel side walls and vertical end walls; walls unthickened, slightly sinuous. Cell shape consistent throughout intercostal zones but length is shorter adjacent to the costal zones. No bulliform cells. Short cell pairs separate successive long cells in the center of the intercostal zones. *Stomata:* shape indistinguishable due to overlapping papillae; four files of stomata in each intercostal zone located in the two files immediately adjacent to the costal zones; stomata separated by single interstomatal long cells. *Intercostal short cells:* paired, tall and narrow silica bodies with smooth outlines; cork cells irregularly shaped, adjacent to the silica cell, present between virtually all long cells in central part of intercostal zones. *Papillae:* small, thickened, cuticular papillae on all intercostal long cells, absent on costal zone; 5–7 papillae located centrally in a single row along with intercostal long cell, particularly those located in the center of the intercostal zones; arrangement on interstomatal long cells is less regular; 4 papillae slightly overlap the subsidiary cells of each stoma from the adjacent interstomatal cells. *Prickles and hooks:* none observed. *Microhairs:* bicellular; basal cell long (more than twice the length of the stomata) and at least twice as long as the tapering, thin-walled distal cell; both cells elongated and hair finger-like in appearance; microhairs restricted to central part of intercostal zones. *Macrohairs:* not present on specimen examined. *Silica bodies:* tall, saddle-shaped, vertically elongated. Costal and intercostal silica bodies similar in shape but costal bodies are considerably larger. *Costal cells:* silico-suberose couples separated by single elongated, rectangular costal long cell. Costal zones associated with third order vascular bundles consist of three files of cells.

Adaxial epidermis (Figure 22*f*). *Intercostal long cells:* lateral cells rectangular with vertical end walls; slightly sinuous walls; separated by cork-silica cell pairs. Central three files consist of bulliform cells; outer surface of central file of bulliform cells minute; lateral two files of bulliform cells with length less than width; often silicified. *Stomata:* absent. *Intercostal short cells:* silico-suberose couples with cork cell

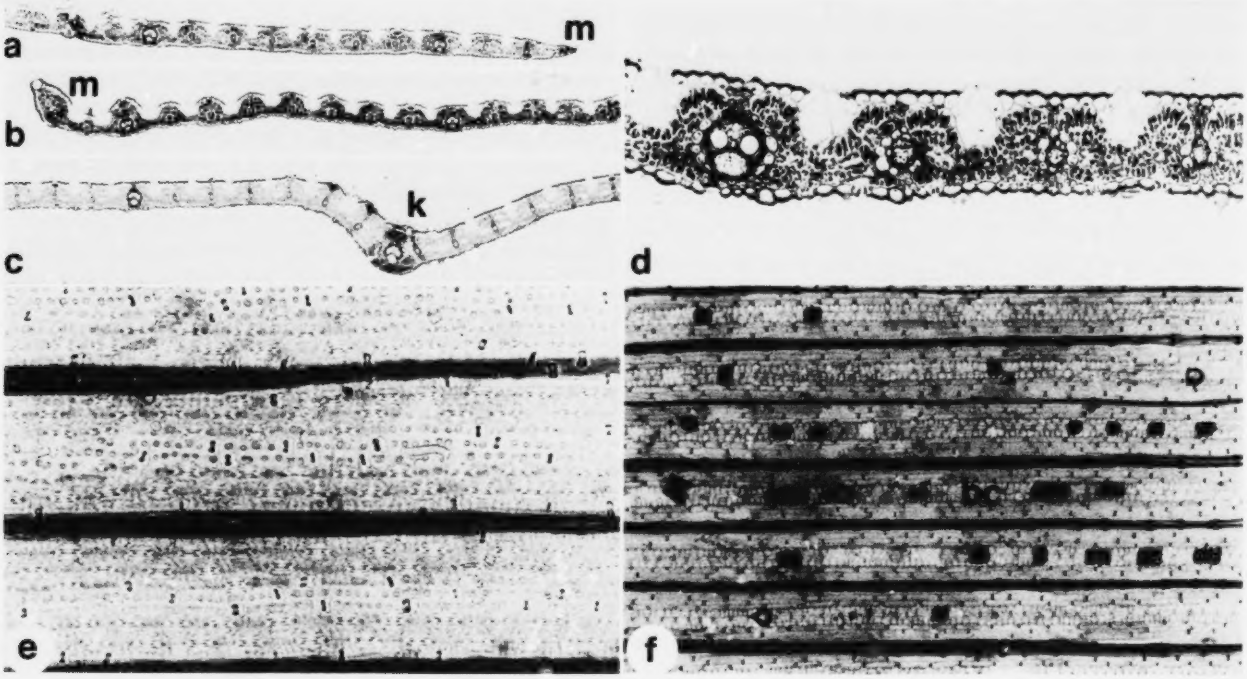

FIGURE 22.—Leaf anatomy of *Bambusa bambos: a*, outline of tapering margin (m) (×59); *b*, outline of opposite, truncated and ribbed margin (m) (×59); *c*, outline of midrib region (k) showing asymmetrical nature of lamina on either side of median vascular bundle (×59); *d*, detail of central part of lamina illustrating the absence of fusoid cell cavities between the vascular bundles (×235); *e*, abaxial epidermis with tall, saddle-shaped silica bodies, papillae, and microhairs (×235); *f*, adaxial epidermis with dark silicified bulliform cells irregularly dispersed along bulliform cell files (bc) (×95). (Based on *Soderstrom and Kulatunge 1762*.)

being tall and narrow. *Papillae:* absent. *Prickles and hooks:* absent. *Microhairs:* none seen. *Macrohairs:* absent. *Silica bodies:* costal silica bodies vertically elongated, saddle-shaped; intercostal silica bodies tall and narrow but much smaller than the costal bodies. *Costal cells:* costal zones consist of single row of cells; alternating silica cells and elongated, rectangular costal long cells.

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1762*, Sri Lanka; US vial no. 428.

DISCUSSION.—The leaf anatomy of this species does not appear to have been described in the literature and further material is required for anatomical study. However, based on the material examined in this study the leaf anatomy of *Bambusa bambos* differs in several important respects from that typical of the Bambusinae, as exemplified by *B. vulgaris*.

1. In *B. bambos* the midrib consists of a single vascular bundle located in a slightly thicker part of the lamina which projects abaxially, is S-shaped and asymmetrical. Midribs with only a single bundle occur in the Arundinariinae and in this respect *B. bambos* resembles this group more than the Bambusinae. The Bambusinae with complex midribs also have the two leaf margins differing considerably in shape. One margin is truncated with well-developed adaxial ribs and furrows associated with the lateral bundles whereas the other margin gradually tapers to a definite point and no ribs or furrows occur in the lateral parts of this side of the lamina. In *B. bambos*, as with those Arundinariinae with simple midribs, this distinction between the left and right margin is not so marked.

2. The Bambusinae typically possess distinct fusoid cell cavities on either side of all vascular bundles, but in *B. bambos* these cavities are virtually absent and only occur sporadically in the region of the midrib. In the Arundinariinae some taxa also lack fusoid cells and this situation is frequently encountered in the Shibataeinae (Nakai) Soderstrom & Ellis. The adaxially located arm cells of *B. bambos* are palisade-like with vertical invaginations as in the Bambusinae. However, the centrally located mesophyll cells are the largest and these obviously replace the fusoid cells and are even arranged in a downward-projecting manner as are the fusoid cells of the typical Bambusinae.

3. Only a single mestome sheath is present in *B. bambos*. In many of the other representatives of the Bambusinae, the inner sheath clearly consists of two layers of thickened cells.

4. The abaxial epidermis of *B. bambos* is very similar to the Bambusinae type except that the papillae are not as long and do not overarch the stomata to the same extent as do those in, for example, *B. vulgaris*. The costal silica bodies, although of similar shape, are separated by much longer costal long cells than is usual in the Bambusinae.

The leaf anatomy of *B. bambos*, therefore, differs considerably from that which is typical of the Bambusinae and anatomically this species bears a strong resemblance to the Arundinariinae. This is of particular significance as *B. bambos* is the type of the genus and, consequently, these observations based on a single specimen will require confirmation before their taxonomic and nomenclatural implications can be assessed.

7. *Bambusa multiplex* (Loureiro) Raeuschel ex J.A. & J.H. Schultes

Bambusa multiplex (Loureiro) Raeuschel ex J.A. & J.H. Schultes in Roemer and Schultes, 1830:1350–1351.

Arundo multiplex Loureiro, 1790:58.—Camus, 1913:132.—Senaratna, 1956:28.

Ludolphia glaucescens Willdenow, 1808:320.

Arundinaria glaucescens (Willdenow) Palisot de Beauvois, 1812:144, 152 [index].—Munro, 1868:22–23.—Alston, 1931:342.

Bambusa nana Roxburgh, 1832:199.—Gamble, 1896:40–41, pl. 38.—Hooker f. in Trimen, 1900:315.—Camus, 1913:121.

Bambusa glaucescens (Willdenow) Siebold ex Munro, 1868:89.—Holttum, 1956a:207–211; 1958:67.

MORPHOLOGY

FIGURES 23, 24

DESCRIPTION.—Plants of unicespitose habit from sympodial, pachymorph rhizomes, with a short neck ~2 cm long, producing dense clumps of closely placed culms. *Culms* weak, cylindrical, hollow, arched above, up to 4.5 m tall, 1–1.5 cm in diam., consisting of ~20 nodes prior to the terminal leafy portion, branching more or less simultaneously from the 6th and above nodes, the lower nodes each with a bud but remaining dormant, the internodes glabrous or sparsely covered with brown antrorse appressed needle-like hairs. *Culm leaves* appressed, deciduous upon growth of branches which force it apart from the culm, more or less triangular with an indistinct external demarcation between sheath and blade except for minute auricles with a few oral setae; blade erect, narrowly triangular, acuminate, glabrous on the outer surface and on the inner surface except for a few scattered appressed hairs; ligule a membrane with irregular margins, less than 0.5 mm long, puberulent on the abaxial surface. *Branching:* central dominant branch produced first, followed in quick succession by germination of proximal buds of several orders, only the central axis and 2 lateral ones greater in size (but not much) than the remaining axes, the whole cluster of branches soon formed up to 20 or more in a whorl. *Foliage leaves* in complements 15–20 cm long, 12–18 cm wide, with 6–13 leaves in the complement, most fully developed blades 7–12 cm long, 1–1.5 cm wide, dark green and glabrous on the upper surface, bluish green and hirtellous on the lower surface, transverse veinlets not manifest, short-petiolate and at length abscissile from the sheath; sheath with small auricles bearing cilia up to 5 mm long; inner ligule a short rim of tissue less than 0.5 mm long, puberulent abaxially. *Inflorescences* at first terminating leafy branches, ultimately resulting in elongate (non-capitate) clusters of several spikelets at the nodes of leafless branches. *Pseudospikelets* sessile, linear-lanceolate, 3–4 cm long, 5–7 mm wide, comprising 2 gemmiferous bracts and up to 10 florets, the uppermost one rudimentary. Empty glumes lacking, disarticulation below the lemma, the florets falling separately. *Spikelets* consisting of up to 10 fertile florets, the lowermost developing first and strongest with reduction upwards; *lemma* linear-lanceolate, ~1.5 cm long, up to 22-nerved, glabrous; *palea* membranous, 2-keeled with the wing-like margins infolded, 16-nerved, each wing with 4 nerves and 6 nerves between the keels (each of which contains 1 nerve), with transverse veinlets; *lodicules* 3, glabrous or with very sparse short cilia, the 2 anterior 4.3–4.7 mm long, 2.1–2.3 mm wide, considerably thickened at anthesis on the lower center half with their wing-like projections extending laterally and at the apex, with up to 12 nerves (some branched), these occurring in the thickened portion and lower part of the membranous apical portion but not extending to the tip, the posterior lodicule a little smaller and narrower, thickened on the lower half on one side and with a fold in the center; *stamens* 6, the anthers maroon, 4.3–4.4 mm long, opening by apical pores, the filaments filiform, free, basifixed; *ovary* obovate (with a narrow base) puberulent on the upper half, with 2 short styles (one of which branches toward the base) and 3 plumose stigmas.

DISTRIBUTION.—This common hedge bamboo is probably native to southeastern Asia. It is now cultivated throughout the tropics of both hemispheres.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Peradeniya, Royal Botanic Gardens, cultivated, *Soderstrom & Kulatunge 1603* (PDA, US); road between Kandy and Peradeniya, cultivated, *Soderstrom & Kulatunge 1604* (PDA, US); Peradeniya. Royal Botanic Gardens, cultivated, "Chinese bamboo, 1 Sept 1867" written in ink on envelope attached to sheet, *s. coll.* (PDA).

DISCUSSION.—The correct name for this commonly cultivated bamboo has been the subject of much debate, centering on the original description of Loureiro, based on material from Cochinchina (1790). Holttum (1956a:207–211) presented the case for using a later name, *Bambusa glaucescens*, and lays out very clearly the arguments for this disposition. He felt that Loureiro's description was not diagnostic enough to identify the species but we disagree with that opinion, as does F.R. Fosberg, with whom we have discussed the case. The synonymy given above is not complete.

In the original description Loureiro gives "cay hop" as the

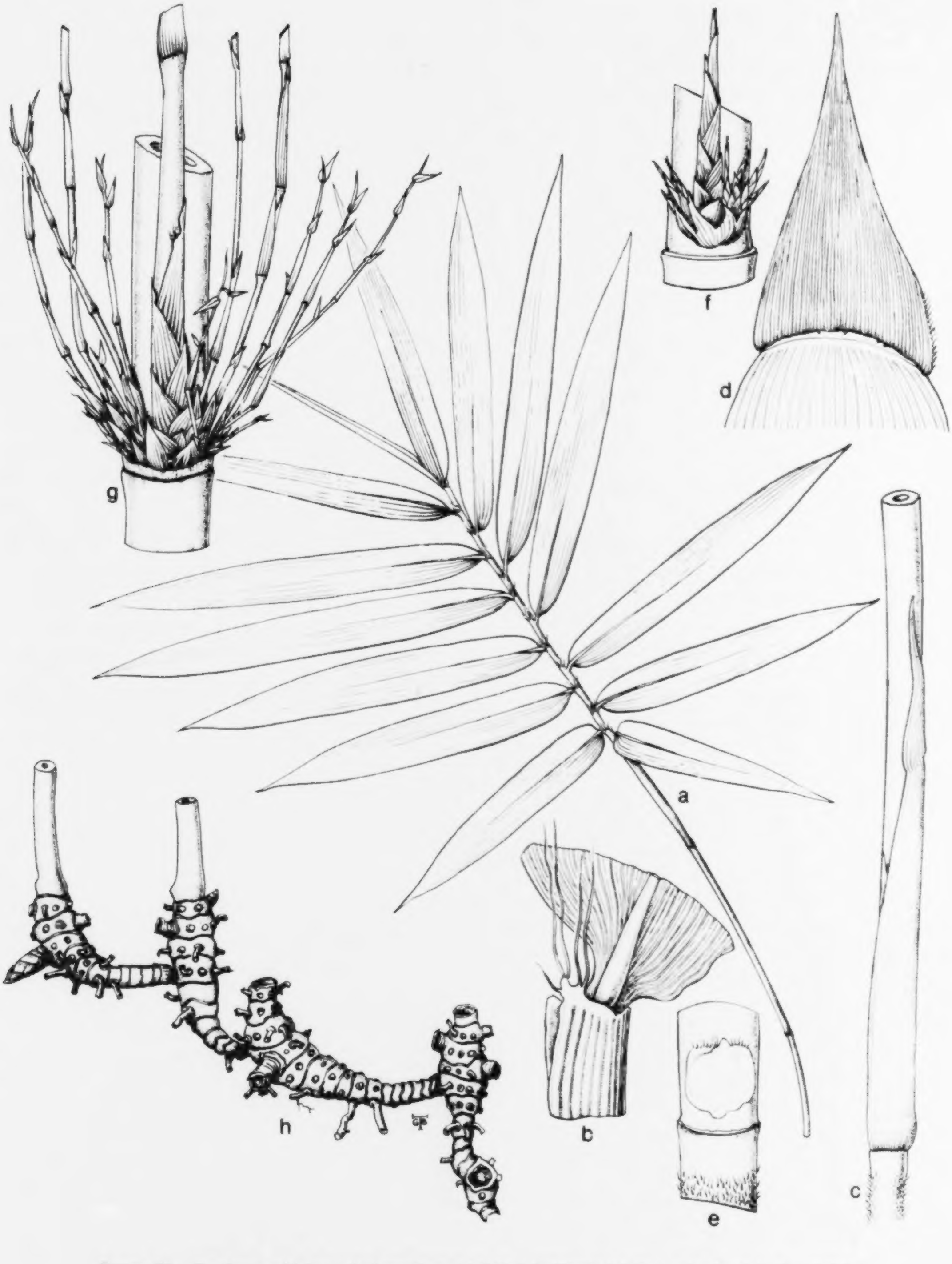

FIGURE 23.—*Bambusa multiplex: a*, leaf complement (×0.6); *b*, leaf ligule (×3.4); *c*, culm sheath in place (×0.6); *d*, culm sheath, adaxial view showing ligule (×1.1); *e*, new culm bud (×1.1); *f*, branch complement, early stage (×1.1); *g*, branch complement, later stage (×1.1); *h*, rhizome (×0.6). (Based on *Soderstrom & Kulatunge 1603*.)

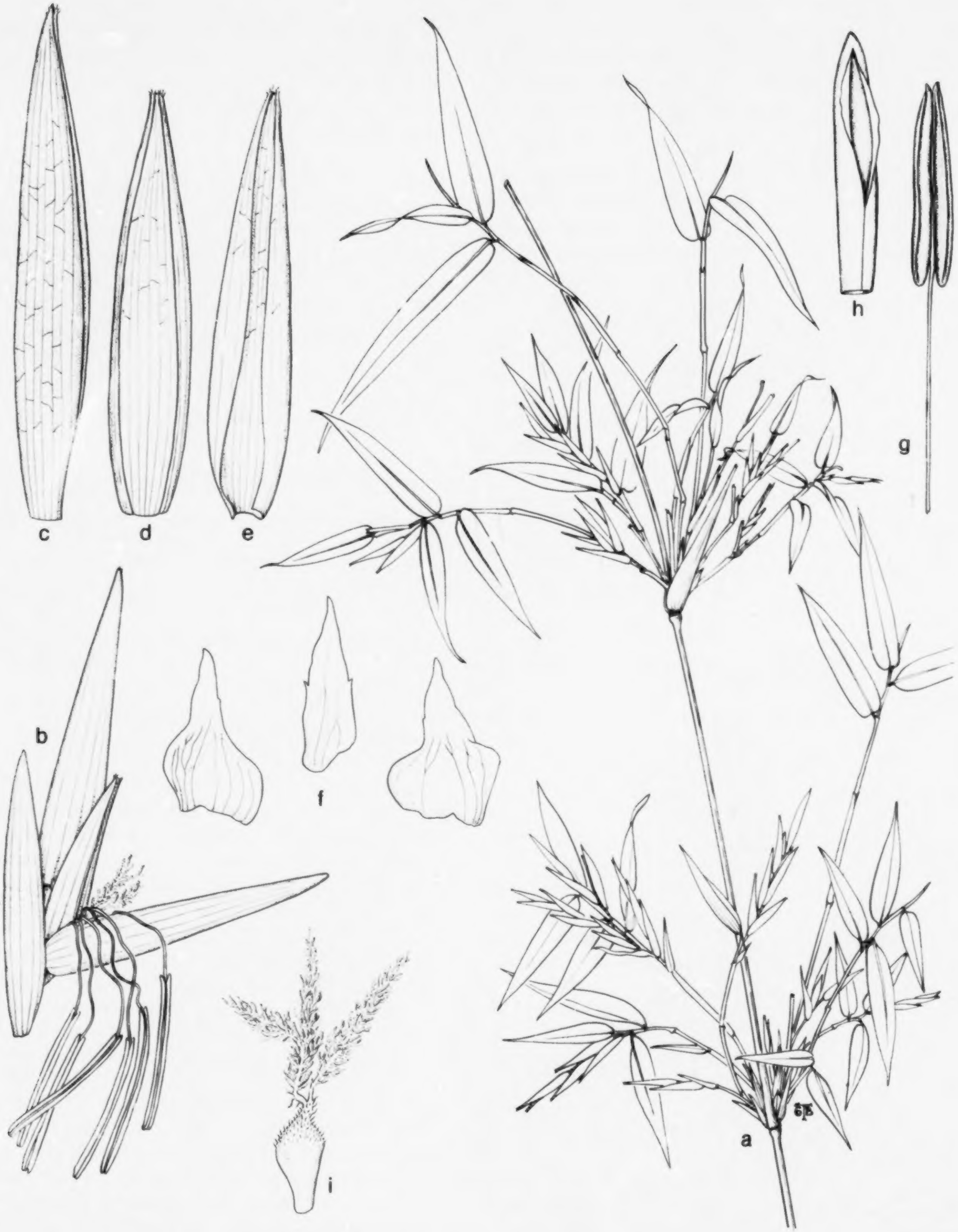

FIGURE 24.—*Bambusa multiplex*: *a*, flowering branches (×0.6); *b*, floret with stamens exserted (×3.6); *c*, lemma (×7); *d*, palea, dorsal view showing keels (×7); *e*, palea, ventral view (×7); *f*, lodicules (×7); *g*, stamen (×7); *h*, apex of dehisced anther (×15); *i*, pistil (×7). (Based on *Soderstrom & Kulatunge 1603*.)

common name for this bamboo in southeast Asia, which is used in hedges. Only three bamboos from the region have "hop" in the common name: *Bambusa flexuosa* Munro, *B. tuldoides* Munro, and the present *B. multiplex*. The first is a thorny species and so can be ruled out, as Loureiro says the new species is unarmed. Holttum points out that both of the other species are used as hedges in Annam, but *B. tuldoides* is generally large in stature and has culms more than one inch in diameter as Loureiro states. Under the description of the flower, the author states that there are three stigmas and they are sessile on the ovary. This is indeed true of *B. multiplex* but not of *B. tuldoides* in which there is a single style that precedes the stigmas. This point, which has not been noted by others, is significant and is further evidence that Loureiro's name should be used.

The plant on which the above description is based has been cultivated at the Rio de Janeiro Botanical Garden for about 10 years, according to the gardener, and flowers throughout the year (probably because it is not trimmed). This same species is commonly employed as a hedge in Kandy and throughout the Central Provinces.

The color of the blades is characteristic: the upper surface is dark green (and glabrous) and the lower surface bluish green (and hirtellous). Spikelets form first on the ends of the primary leafy twigs, but later these twigs rebranch and form spikelets. Eventually the whole whorl of branches contains spikelets only and no further leaves.

We made no anatomical study of the leaves of *Bambusa multiplex*.

8. *Bambusa vulgaris* Schrader ex Wendland

Bambusa vulgaris Schrader ex Wendland, 1810:26, pl. 27.—Munro, 1868:106–108.—Beddome, 1873:232.—Gamble, 1896:43–45, pl. 40.—Hooker f. in Trimen, 1900:314.—Camus, 1913:122–123, pl. 76: fig. A.—Senaratna, 1956:27–28.

Bambusa arundinacea Retzius [as *Bambos*], 1789:24.—Moon, 1840:26 [teste Stafleu and Cowan, 1981:566].—Willdenow, 1799:245 [as *Bambusa*].

Bambusa thouarsii Kunth, 1830:323, pl. 73, 74.

Bambusa surinamensis Ruprecht, 1839:139, pl. 11: fig. 49.

MORPHOLOGY

FIGURES 25–28

DESCRIPTION.—Plants of unicespitose habit from sympodial, pachymorph rhizomes, producing more or less open clumps of closely, but not densely, placed culms, the culms strong, cylindrical, hollow, erect and arched above, 15–20 m tall, 4–10 cm diam. with walls 9–15 mm thick, branching from the lower nodes, slightly zig-zag, the nodes biannular with a strong ridge at the point of sheath attachment and a finely marked upper ridge, the internodes 20–45 cm long, glabrous or with a waxy surface and with appressed brownish black, deciduous hairs, especially toward the summit. *Nodes* containing a single ovate, obtuse, or obtusely acuminate bud, this shiny and strongly compressed dorsally. *Culm leaves* appressed, the lower short, the higher 30–45 cm long, deciduous, more or less broadly triangular, the juncture of sheath with blade rising toward the middle, the blade ~$^{1}/_{4}$ the length of the culm leaf, the sheath covered with patches of dense blackish brown hairs over the back but the margins glabrous in a broad band, the incurved shoulders bearing broad, dark brown, falcate-spreading auricles with long cilia; blade erect, persistent, broadly triangular with a cucullate tip, glabrous on the smooth back or with scattered, appressed dark brown hairs, the inner surface strongly ribbed with dense, dark brown appressed hairs (spicules) at the base and less so upwards toward the center; ligule a glabrous membrance ~1 mm long with dentate, ciliolate margins. *Branching:* central dominant branch produced with secondary branches from the lowermost nodes, each axis segmented on the lower part and the whole becoming thickened and bulbous, the secondary branches at maturity assuming a lateral position to the central one, the secondary branches producing tertiary branches from their lower nodes, and so on. *Foliage leaves* in complements up to 0.5 m long and 30 cm wide, with 8 or 9 leaves, most fully developed blades up to 30 cm long, 4.5 cm wide, linear-lanceolate with a rounded to cuneate base and acuminate at the tip, the edges smooth or only slightly serrate, pale green and glabrous on both surfaces, the midrib elevated and prominent on the lower surface, transverse veinlets not manifest except abaxially in young blades, short-petiolate and at length abscissile from the sheath; sheath glabrous or with sparse, dark brown appressed hairs toward the summit; inner ligule a truncate rim ~0.4 mm long, glabrous on the adaxial surface, puberulent on the abaxial surface; outer ligule a hard, glossy flap of tissue 1 mm long or less with a ciliolate margin, prominent on either side of the midrib. *Inflorescences* at first terminating leafy branches, ultimately resulting in elongate clusters of few spikelets or semi-capitate clusters of several spikelets at the nodes of leafless branches. *Pseudospikelets* sessile, lanceolate, 16–19 mm long, comprising 2 gemmiferous bracts, an empty glume, and up to 7 florets, the uppermost one rudimentary, with disarticulation below the lemmas, the florets falling separately; *glume* broadly ovate, apiculate, 12-nerved with some transverse veinlets, glabrous; *lemmas* ovate-triangular, apiculate, 10–14-nerved with some transverse veinlets, ~9–11 mm long, glabrous; *palea* membranous, 2-keeled with the wing-like margins infolded and sulcate between the keels, 7-nerved (2 keels + 1 nerve in each wing + 3 nerves between the keels), glabrous except for the keels ciliate on the upper part, equal to or a little longer than the lemma; *lodicules* 3, ovoid, membranous, ciliate on the upper margins, the anterior pair ~2.6 mm long, 1–3-nerved, the posterior a little smaller; *stamens* 6, the filaments separate or in some florets loosely connate, anthers orange, 6–7 mm long, basifixed, the filament attached to the connective on about the lower $^{1}/_{7}$th, the connective projecting as a minute ciliolate point at the apex; *ovary* terete, glabrous below, narrowed upward and hardened,

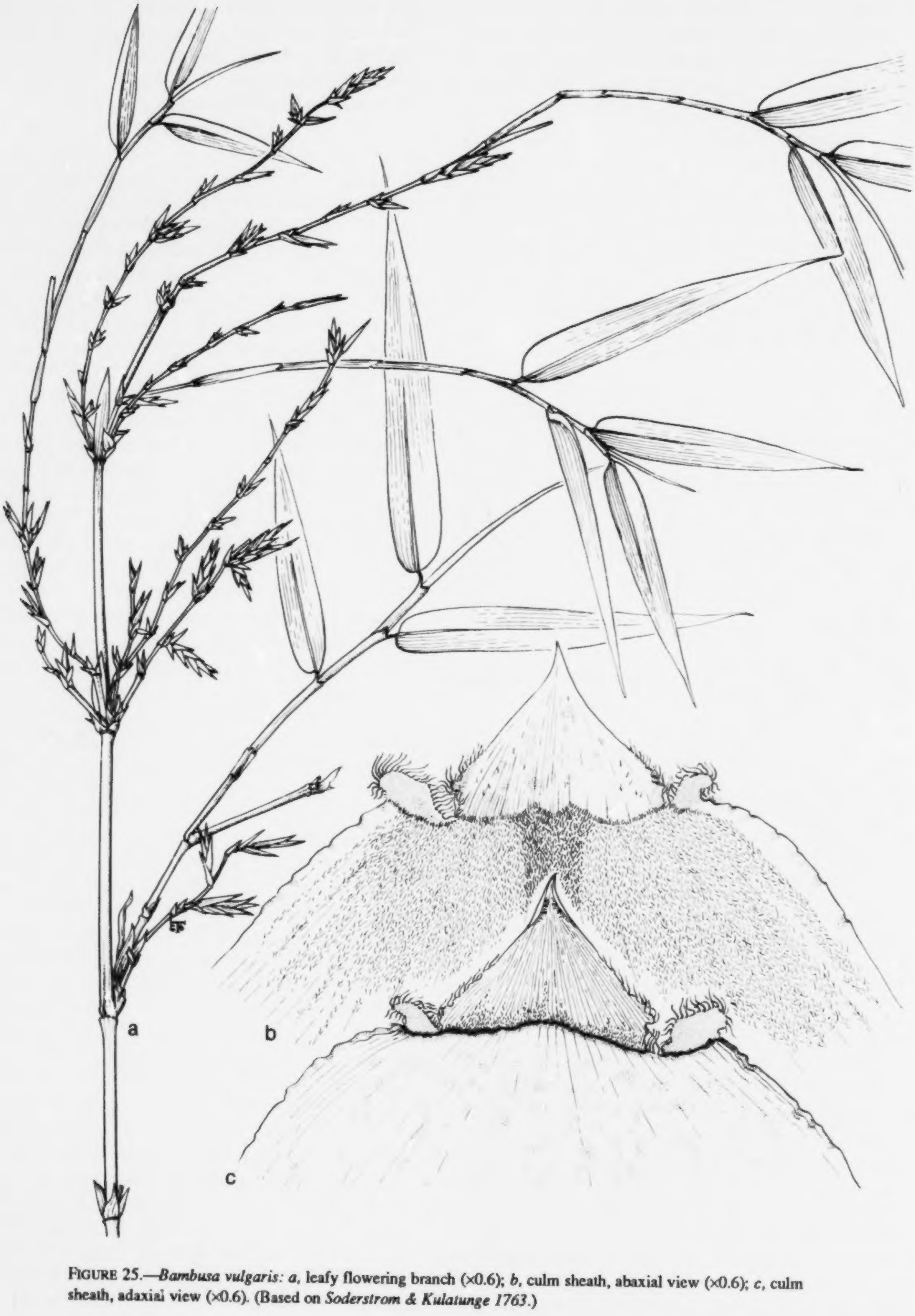

FIGURE 25.—*Bambusa vulgaris: a*, leafy flowering branch (×0.6); *b*, culm sheath, abaxial view (×0.6); *c*, culm sheath, adaxial view (×0.6). (Based on *Soderstrom & Kulatunge 1763.*)

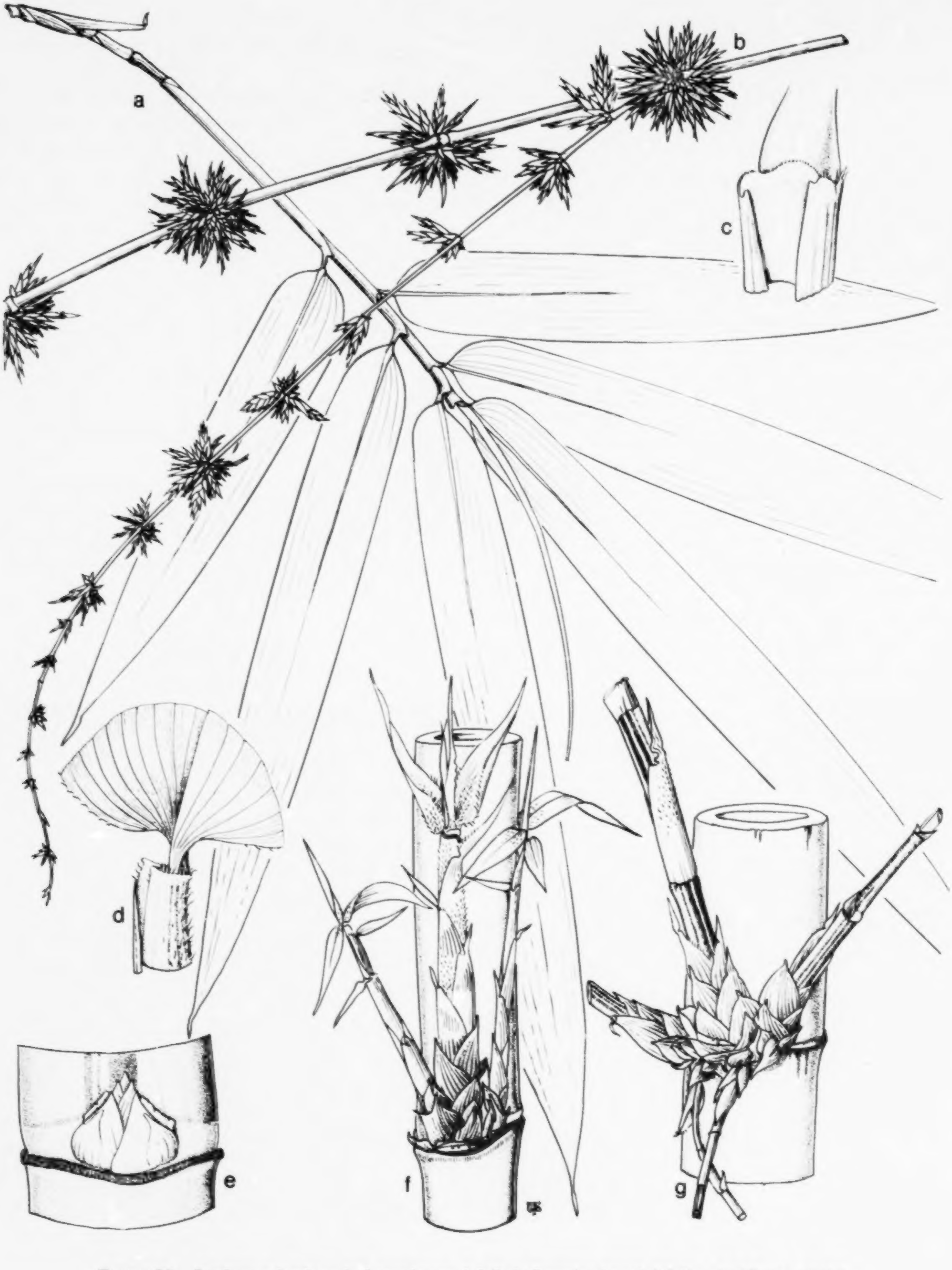

FIGURE 26.—*Bambusa vulgaris: a*, leaf complement (×0.6); *b*, flowering branch (×0.6); *c*, leaf ligule, adaxial view (×6); *d*, leaf ligule, side view (×3.6); *e*, bud of new culm (×0.6); *f*, young branch complement (×0.3); *g*, mid-culm branch complement (×0.3). (Based on *Soderstrom & Kulatunge 1763*.)

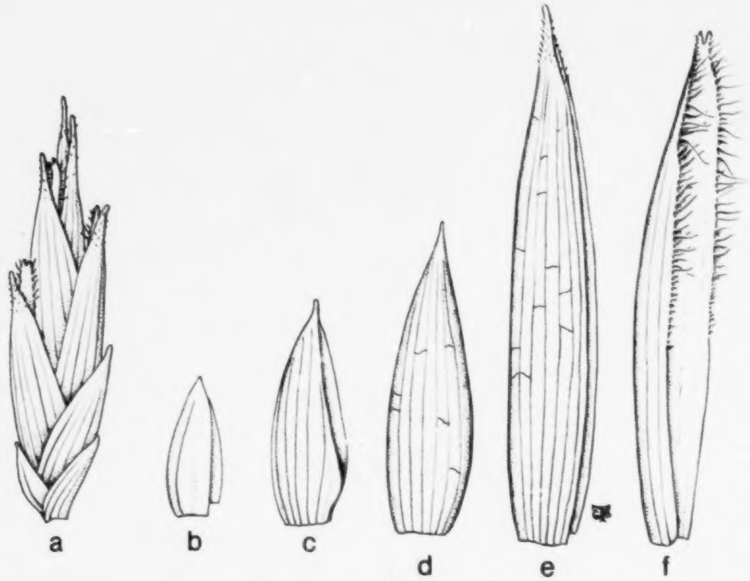

FIGURE 27.—*Bambusa vulgaris*, spikelet dissection: *a*, pseudospikelet (×3.8); *b*, glume I (×7.7); *c*, glume II (×7.7); *d*, glume III (×7.7); *e*, lemma (×7.7), *f*, palea (×7.7). (Based on *Soderstrom & Kulatunge 1763*.)

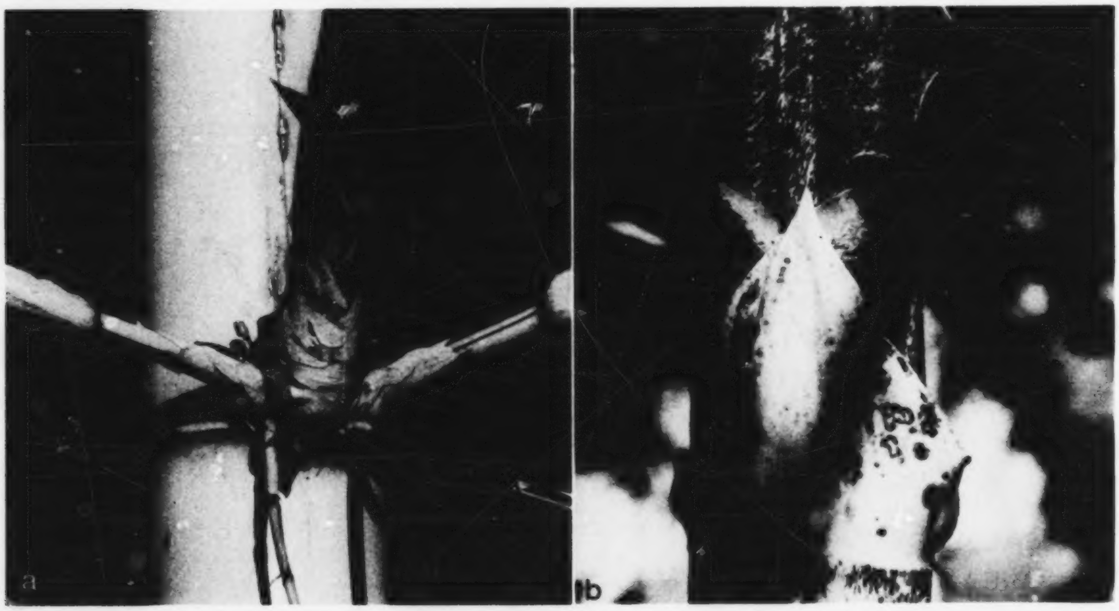

FIGURE 28.—Field photographs of *Bambusa vulgaris* near Kandy: *a*, branching at a mature node. Note the main primary branch (striped), the secondary branches produced from it, and from these, smaller, third order branches, the branching directly from the nodal line in this genus; *b*, new culm leaves. Facing is the erect blade, opposite this are the overlapping margins of the next higher culm leaf. Note the prominent ciliate auricles that are part of the sheath. (Photographs based on *Soderstrom & Kulatunge 1763*.)

extending into an elongate style terminating in 1–3 plumose stigmas, the upper portion of the ovary and style pubescent; *Fruit* unknown.

DISTRIBUTION.—Country of origin unknown, but probably originally from tropical Asia. Now cultivated throughout the Old and New World Tropics.

SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Kandy, near the Malwatte Temple road to Hillroad College, *Soderstrom & Kulatunge 1763* (PDA, US). NUWARA ELIJA DISTRICT: Nuwara Elija road near Boralanda, *Gould 13353* PDA, US), *13354* (PDA, US). Locality Unknown: Ambagamuwa, Jul 1855, *s. coll., C.P. 3252* (PDA); "leg. Thwaites" written in ink on label, *C.P. 3252* (US ex W); Thwaites *C.P. 3252* (US ex P [Caen]).

DISCUSSION.—We have borrowed from the excellent and detailed descriptions of this species found in McClure (1955) and Backer and van der Brink (1968). The synonymy given above is incomplete.

The culms of *Bambusa vulgaris* in the natural form are a smooth and polished dark green. A golden form also occurs and is widely planted; it has green stripes of varying widths that alternate from one internode to the other.

ANATOMY

FIGURE 29

DESCRIPTION.—*Leaf anatomy in transverse section. Leaf outline:* expanded and flat; asymmetrical about the midrib (Figure 29*b*) and probably also with the two margins differing in shape. Leaf thickness ~150 µm. *Ribs and furrows:* adaxial and abaxial surfaces midway between midrib and margin virtually flat with no undulations associated with the vascular bundles (Figure 29*c*); the lamina close to one margin and immediately to the same side of the midrib with well-developed adaxial ribs and furrows (Figure 29*a,b*); these ribs rounded, and separated by wide furrows. *Midrib:* abaxially projecting, broadly S-shaped, asymmetrical structure with complex vasculature (Figure 29*b*); two adaxial bundles and several abaxially located bundles included and embedded in wide sclerenchyma girder. *Vascular bundle arrangement:* 9 first rder vascular bundles in half the lamina and presumably 17 n entire blade; no second order bundles; 9 third order bundles etween successive first order vascular bundles. All bundles ocated closer to the abaxial surface (Figure 29*c*). *Vascular undle description:* third order bundles elliptical; xylem and hloem clearly distinguishable (Figure 29*c*); first order bundles ound; lysigenous cavity and protoxylem present; metaxylem essels wide, unthickened and circular. *Vascular bundle sheaths:* double, even around third order bundles. Outer sheath round or circular; entire around third order vascular bundles but with wide abaxial and slight adaxial interruptions in the sheaths of first order bundles (Figure 29*c*); no extensions. Outer bundle sheath cells of third order bundles rounded and somewhat larger than those of the first order bundles; outer bundle sheath cells of first order bundles tend to be elliptical, rather small, with unthickened walls and without chloroplasts; numerous (~10) per third order bundle and more than 17 per first order bundle. Inner sheath complete; double around first order bundles; cells with heavily but uniformly thickened walls (Figure 29*c*). *Sclerenchyma:* adaxial girders narrow and deep; abaxial girders wide and short, particularly in association with first order bundles; no sclerenchyma present between the bundles. Minute sclerenchyma cap in margin (Figure 29*a*). *Chlorenchyma:* non-radiate, distinct, rounded, downward projecting fusoid cavities on either side of all vascular bundles (Figure 29*c*); adjacent fusoid cells separated by 2–3 mesophyll cells; adaxial layer of arm cells with conspicuous invaginations from the lower cell wall; all other arm cells situated above the fusoid cavities also with more prominent vertical invaginations but lateral and dorsal invaginations also present; arm cells located below the fusoid cells with shorter invaginations projecting equally from all the cell walls (Figure 29*c*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups distinct, raised above level of epidermis, fan-shaped and occupy half leaf thickness (Figure 29*c*); central cell shield-shaped; 1 or 2 bulliform cells present on either side of the enlarged central cell; no cuticle developed on outer surface of the bulliform cells. Outer walls of remaining adaxial epidermal cells covered by a continuous, thickened cuticle; costal and intercostal cells of similar size and shape; no macrohairs, prickles or papillae; stomata present. *Abaxial epidermis:* no bulliform cells present; each cell with individually thickened cuticle projected into narrow cuticular papillae, either single or bifurcate; no macrohairs or prickles.

Abaxial epidermis (Figure 29*d*). *Intercostal long cells:* elongated with parallel side walls and vertical end walls; walls unthickened, deeply sinuous. Cell shape varies across intercostal zones, the cells being more elongate in the central files. No bulliform cells. Short cell pairs or stomata separate successive long cells. *Stomata:* overlapping papillae conceal shape; 4 rows of stomata on either side of each costal zone, i.e., 8 per intercostal zone; stomatal files adjacent to one another; one interstomatal long cell between successive stomata. *Intercostal short cells:* paired; cork cell tall and narrow with somewhat crenate outline enfolding smaller and narrower silica cell, present between all long cells in central files of intercostal zones. *Papillae:* small, thickened, cuticular, present on all long cells including the costal zones; 6–9 papillae in single row on each long cell in center of intercostal zones, somewhat irregular in arrangement on interstomatal long cells but usually in two distinct rows; 4–6 papillae overarch stomata. *Prickles and hooks:* none observed. *Microhairs:* elongated, finger-like; total length of hair about 4× length of the stomata; basal and distal cells almost equal in length; distal cell thin-walled and normally collapsed. Microhairs confined to the center of the intercostal zones. *Macrohairs:* absent. *Silica bodies:* costal bodies vertically

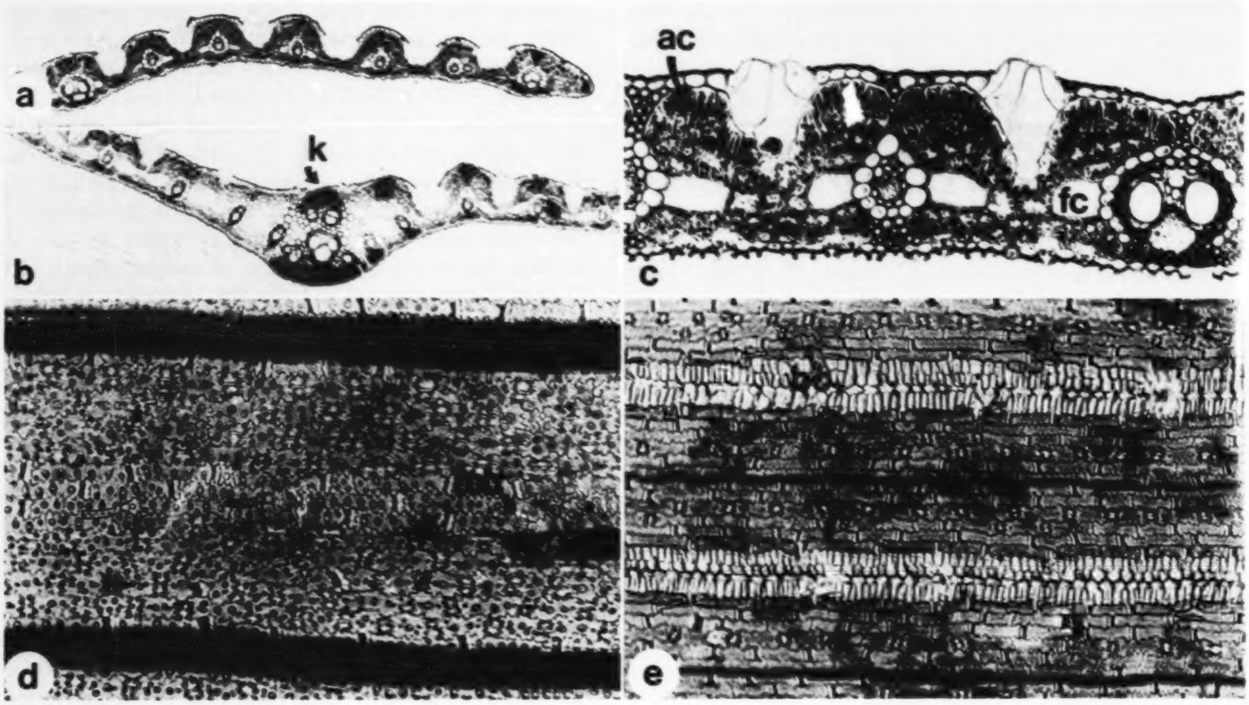

FIGURE 29.—Leaf anatomy of *Bambusa vulgaris: a,* ribbed lateral part of one side of leaf blade (×58); *b,* outline of midrib region (k) showing complex vasculature of keel and asymmetrical nature of blade on either side of the keel (×58); *c,* anatomical detail showing vertical, adaxial arm cell invaginations (ac), fusoid cavities (fc), vascular bundle structure, and papillae on abaxial epidermis (×230); *d,* abaxial epidermis with tall, saddle-shaped silica bodies, microhairs (mh), and papillae overlying the stomata (×230); *e,* adaxial epidermis with files of bulliform cells (bc) with microhairs on their edges and silico-suberose pairs (×145). (Based on *Soderstrom & Kulatunge 1763.*)

elongated, tall, saddle-shaped; with granules; same width as costal long cells. Intercostal bodies much smaller, tall and narrow with smooth outlines; enfolded by cork cells. *Costal cells:* silica cells alternate with elongated, rectangular long cells with sinuous walls; third order vascular bundle costal zones of 1–3 files of cells.

Adaxial epidermis (Figure 29*e*). *Intercostal long cells:* lateral cells of intercostal zones rectangular with slightly sinuous walls; separated by stomata or cork-silica cell pairs. Central 3 or 4 files consist of bulliform cells arranged in a complex interlocking manner; 2 or 3 files of very short and wide cells with triangular apices; remaining file (representing the large shield-shaped cell as seen in transection) with very small outer surface; usually diamond-shaped and fitting between triangular lateral cell faces. *Stomata:* two files of stomata present between bulliform cell files and costal zones; papillae or flanges on the subsidiary cells conceal stomatal shape; separated by single interstomatal long cells. *Intercostal short cells:* silico-suberose couples with both cells being tall and narrow; situated between all long cells. *Papillae:* absent except for small flange-like projections overarching the stomata. *Prickles and hooks:* none observed. *Microhairs:* present on either side of bulliform cell files; elongate, finger-like. *Macrohairs:* absent. *Silica bodies:* tall and narrow to tall, saddle-shaped. *Costal cells:* costal zones indistinct and very narrow (1–3 files of cells); elongate, rectangular long cells with sinuous walls alternate with silico-suberose couples; both cells tall and narrow.

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1763,* Sri Lanka; US vial no. 429.

DISCUSSION.—The leaf anatomy of *Bambusa vulgaris* has been examined and described by both Brandis (1907) and Metcalfe (1960), and the observations of this study agree very closely with these previous ones. The only significant difference is that Metcalfe observed the microhairs to have deposits of silica on the transverse walls between the two cells while no such deposits were seen in the present study. Metcalfe also noted abundant hooks and small prickles in the abaxial intercostal zones.

The leaf blade anatomy of *B. vulgaris* is typical of that of the majority of the giant, erect, woody, clump-forming bamboos, which belong to the subtribe Bambusinae of the

Bambuseae. This grouping includes such well-known genera as *Bambusa, Dendrocalamus, Oxytenanthera* Munro, and *Oreobambos* K. Schumann, all of which occur in the tropical lowland areas of Africa and Asia.

The anatomy of all these bamboos is characterized by a well-developed, abaxially projecting, S-shaped, asymmetrical midrib with complex vasculature and, at least, two adaxially positioned vascular bundles. The lamina immediately adjacent to one side only of this midrib is ribbed, as is the region of the margin on the same side. The remainder of the lamina is without ribs or furrows. Rounded, downward projecting fusoid cell cavities occur on either side of each vascular bundle (except sometimes in the region close to the margins). Adjacent fusoid cells are separated by 2–3 arm cells of the mesophyll. The arm cells located above these fusoid cells are arranged in 3 palisade-like layers and the invaginations from the lower side of all these cells are vertical and very prominent, particularly those of the uppermost layer. The bulliform cells occur in short, distinct groups of 3–4 cells with the central shield-shaped cell being by far the largest and occupying about half the leaf thickness. Abaxial cuticular papillae are present on all the epidermal cells and are not of the refractive type. The papillae overarch the laterally located stomata but in the center of the intercostal zones the papillae are arranged in a single file of at least 6 erect papillae positioned in the center of each long cell. Elongate, rod-like microhairs are present which are at least twice as long as the length of the stomata. The costal silica bodies are vertically elongated, tall, and saddle-shaped. On the adaxial epidermis the central 2–4 files of intercostal cells are bulliform cells. In surface view these cells are tall and short and angular in outline. They are arranged in an alternating, interlocking fashion. No adaxial papillae are present except sometimes in association with the stomata.

The anatomy of *B. vulgaris*, therefore, corresponds very closely indeed to this group of woody bamboos from Asia and Africa. This appears to confirm its classification at the subtribal level. However, there is very little to distinguish this species from many of the other genera and species also included in the Bambusinae. Many of these closely related species, which possibly constitute only a single genus, do possess numerous epidermal hooks and even prickle-like macrohairs which, at first glance, appear to be an important difference. However, the distribution of these hooks across the width and along the length of even a single leaf is inconsistent and their presence in surface view depends on the position from which the epidermal scrape was prepared. Thus Metcalfe (1960) notes that hooks are abundant in the intercostal zones of *B. vulgaris*. No taxonomic significance should, therefore, be attached to the presence or absence of these hairs. In addition, these hooks merely replace the intercostal short cells and, consequently, the basic configuration of the epidermal cellular pattern is altered very little.

The leaf anatomy of *B. vulgaris* confirms its placement in the *Bambusa* complex and also corroborates the very close morphological resemblance of most of the species placed in this subtribe. The advisability of recognizing all these taxa as subgenera of *Bambusa* deserves investigation and appears to be supported by the leaf anatomy.

Genus *Dendrocalamus* Nees von Esenbeck

Dendrocalamus Nees von Esenbeck, 1835:476.

TYPE SPECIES.—*Dendrocalamus strictus* (Roxburgh) Nees von Esenbeck, 1835:476.

DIAGNOSIS.—In the wide sense similar to *Bambusa* but with the following tendencies: culm sheath blades generally reflexed; inflorescences densely capitate; all fertile florets disarticulating between the very short rachilla segments, the terminal rudiment usually lacking; lodicules often absent; stamens often monadelphous and anthers penicillate; and stigma single, elongate.

DISTRIBUTION.—Tropical Asia. The genus in its widest sense contains several dozen species.

9. *Dendrocalamus cinctus* R.B. Majumder ex Soderstrom & Ellis, new species

Dendrocalamus sp. nov. a *D. pendulus* Ridley similis sed spiculae longiore et non atque glabrae et nitidae.

TYPE SPECIMEN.—SRI LANKA. ANURADHAPURA DISTRICT: Ritigala Strict Natural Reserve, Weweltenna Plain, exposed rocky area, alt. 1940 ft. [590 m], 28 Sep 1972, *A.H.M. Jayasuriya 868* (Holotype: US, sheet no. 2768725; isotype, PDA.).

MORPHOLOGY

FIGURES 30–32

DESCRIPTION.—Plants of unicespitose habit from sympodial, pachymorph rhizomes, producing erect, hard culms up to 6 m tall, ~2.5 cm at the base, the culms hollow with relatively thick walls, the inside surfaces covered with powder, internodes dull green and finely roughened to yellowish green, smooth and shiny with some appressed hairs toward the summit. *Culm leaves* deciduous; sheath hard, brittle, green or greenish yellow, becoming brown, finely roughened with appressed dark brown hairs (spicules), these sparse below, abundant toward the summit where ceraceous, the upper margin recurved, continuous with the blade and extended on both sides into long, often overlapping, appendages, the entire margin bearing short, pale oral setae, deciduous, abscissile above the node, leaving a thick girdle; *blade* reflexed, persistent, over half as long as the sheath, 15–25 cm long, ~2 cm wide, lanceolate, narrowing below to a truncate base and tapering above to an acuminate tip, glabrous on the upper surface except for a patch of brown appressed spicules toward the summit in the center, the primary veins not prominent nor

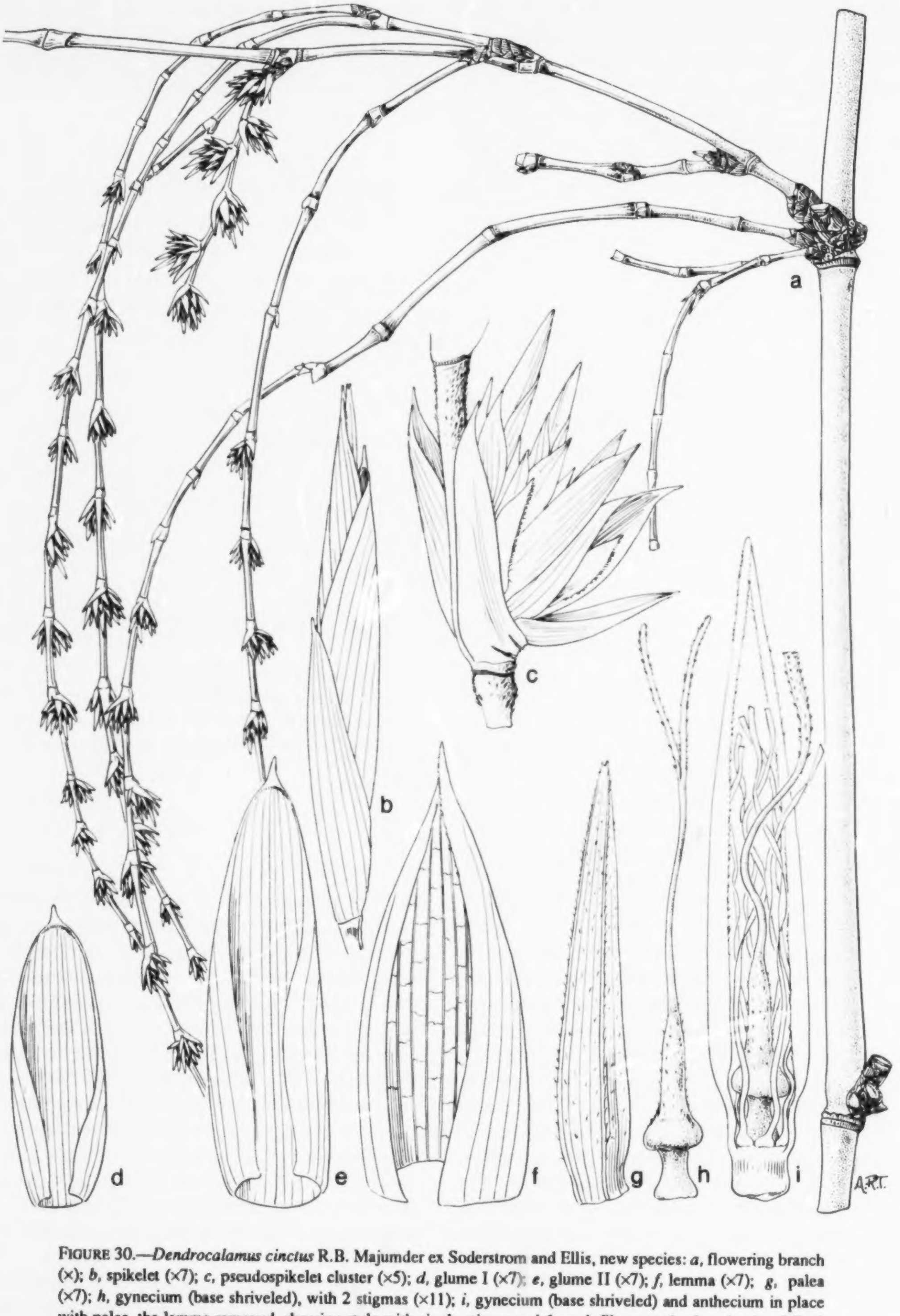

FIGURE 30.—*Dendrocalamus cinctus* R.B. Majumder ex Soderstrom and Ellis, new species: *a*, flowering branch (×); *b*, spikelet (×7); *c*, pseudospikelet cluster (×5); *d*, glume I (×7); *e*, glume II (×7); *f*, lemma (×7); *g*, palea (×7); *h*, gynecium (base shriveled), with 2 stigmas (×11); *i*, gynecium (base shriveled) and anthecium in place with palea, the lemma removed, showing style with single stigma and 6 weak filaments (anthers having fallen) (×3.7). (Based on *Jayasuriya 868*.)

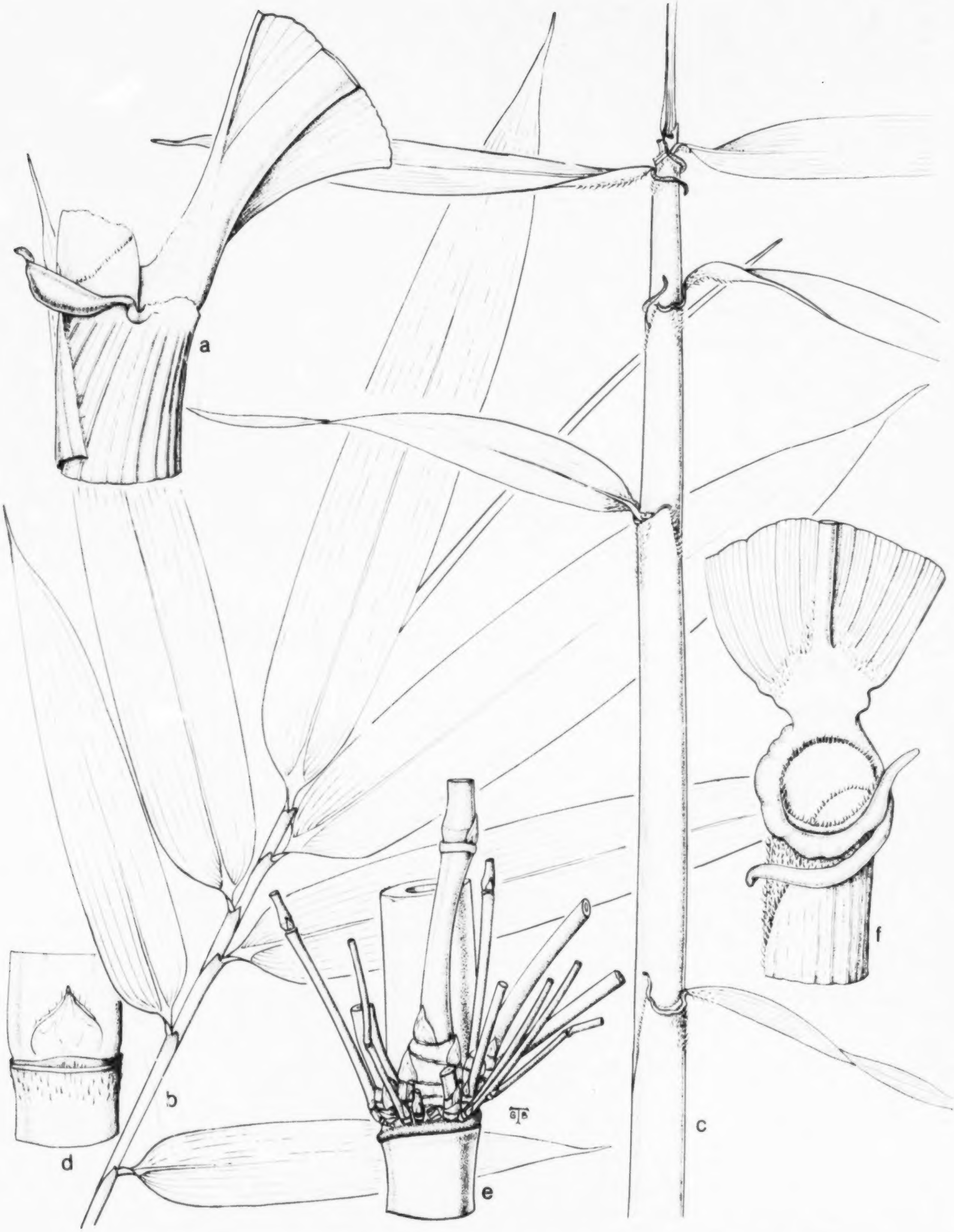

FIGURE 31.—*Dendrocalamus cinctus* R.B. Majumder ex Soderstrom & Ellis, new species: *a*, leaf ligule (×7.2); *b*; leaf complement (×0.6); *c*, young leafy shoot (×0.6); *d*, bud on new culm (×1.8); *e*, mid-culm branch complement (×1.8); *f*, culm sheath with auricles (×3.6). (Based on *Soderstrom & Kulatunge 1764*.)

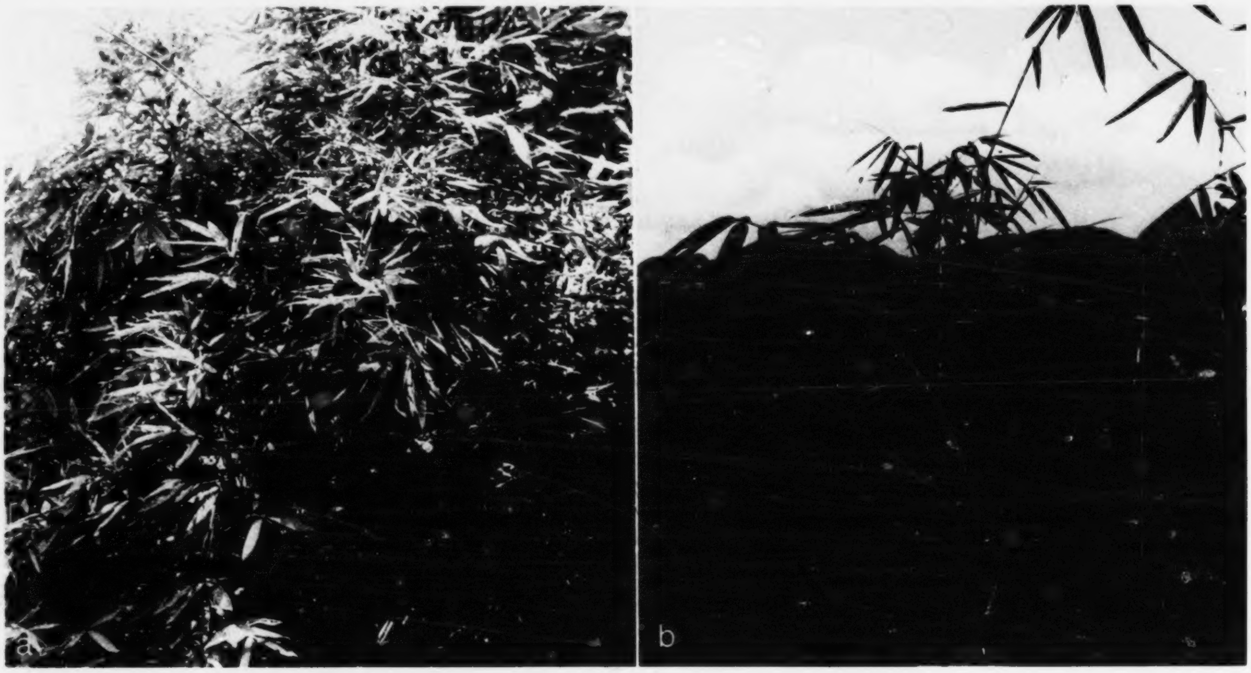

FIGURE 32.—Field photographs of *Dendrocalamus cinctus* R.B. Majumder ex Soderstrom & Ellis, new species, Bambarakelle Hill, Tendeniya, east of Kandy: *a*, leafy culms; *b*, upper part of newly branched culm. (Photographs show *Soderstrom & Kulatunge 1764*.)

tessellate, the lower surface glabrous except for the apically directed appressed brown spicules on the internerves at the base, the primary veins and tessellation manifest; *outer ligule* lacking; *inner ligule* manifest from side view, ~1.3 mm long, glabrous adaxially, whitish, ceraceous abaxially, the margin denticulate. *Nodes* containing a single branch bud covered at the base by the girdle, very broad and extending to half or more of the circumference of the culm, the prophyllum glabrous except for the very finely puberulent upper margin, upper ridge indistinct on the larger nodes, distinct on the biannular nodes of the smaller branches. *Branching* from the nodal line: primary and 2 secondary branches produced about the same time and subequal in size, these followed by further orders to produce a cluster of branches, sometimes the secondaries produced and the primary aborted. *Foliage leaves* in complements 20–25 cm long, ~15 cm wide, with 7 or 8 leaves; *blades* of smaller branches 1.5–2 cm wide, 18–20 cm long, in the primary branches up to 30 cm long, 4.5 cm wide, broadly lanceolate, constricted above to an acute tapering tip, narrowed below to a short petiole, at length abscissile from the sheath, glabrous on both surfaces with smooth or serrulate edges, the midvein but not primary veins manifest on the upper surface, midvein prominent and elevated on the lower surface, primary veins and tessellation manifest; *sheath* glabrous, recurved at the summit and often extending into lateral appendages in the most fully developed leaves; *outer ligule* a hard, stramineous, glabrous rim less than 1 mm long on either side of the petiole, with a ciliolate margin; *inner ligule* a truncate rim with denticulate upper margin manifest from side view, ~2 mm long, puberulent on the abaxial surface, glabrous on the adaxial. Culm with flowering branches 1.5 cm diameter, bearing at the nodal line a primary branch and complex subsidiary branches subtended by a persistent ring and the fallen sheath, the culm glabrous except for the ultimate small scabrid or pubescent branchlets. *Inflorescences* developing by way of pseudo spikelets, resulting in dense clusters at the nodes of leafless branches. Early clusters of pseudospikelets subtended by a firm bract (prophyllum), and the cluster consisting of numerous spikelets, accompanied by firm prophylla and bracts, these clusters ~1.5 cm diameter. *Spikelets* ~10–12 mm long, 1-flowered, with two glumes, lemma, palea, 6 stamens, and single style and stigma; lower glume ovate, 7 mm long, glabrous, 13-nerved; upper glume 9.4 mm long, glabrous, 16-nerved; *lemma* broadly triangular and narrowed to an acute apex, 11 mm long, glabrous, 16-nerved with numerous transverse veinlets; *palea* thin, narrowly triangular, slightly puberulent on the upper part of the keels, otherwise glabrous with two thin nerves between the keel and one in each wing; lodicules lacking; *andrecium–stamens* 6, the filaments united with a thin, fragile tube (?), anthers orange, ~6 mm long;

gynecium–ovary urn-shaped, narrowed upward into a single style, the latter puberulent on the upper part and terminating in 1–2 stigmas.

DISTRIBUTION.—Endemic to Sri Lanka. This bamboo was collected by A.H.M. Jayasuriya in dry scrub forest in Ritigala Strict Natural Reserve. According to the collector, the bamboo has not been introduced but forms a natural part of the vegetation in this dry area, along with another bamboo.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Teldeniya, east of Kandy. Bambarakelle Hill near the Bambarakelle Temple, on north slope in crevices of granite outcrop, alt. ~600 m, 3 Dec 1969, *T. R. Soderstrom & S. Kulatunge 1764* (FDA, US). ANURADHAPURA DISTRICT: Ritigala Strict Natural Reserve, eastern slope of Andikanda, *Jayasuriya 1064* (PDA, US).

DISCUSSION.—As the holotype of *Dendrocalamus cinctus* we have selected the sheet at US, which has a larger culm that shows the powder on the inside walls, and a well-developed girdle at the node at which several flowering branches are borne. In both cases the branches are old and long past flowering.

The flowering material is unlike any bamboo known in Sri Lanka or India and the closest match that we have been able to find is with the Malayan endemic *D. pendulus* Ridley, but the two are not conspecific and their relationship may be only superficial. Soejatmi Dransfield (pers. comm.) indicates that the new species may also share affinities with the Malayan taxa *D. dumosus* (Ridley) Holttum and *D. elegans* (Ridley) Holttum. All of these species have single-flowered spikelets, but the spikelets of the Sri Lanka species are a little larger and not so smooth and shiny as the Malayan one. Both have similar culm branches and a persistent culm sheath base below the node. Good collections of the vegetative structures of *D. cinctus* are needed, especially the culm leaves, which are so important in identification at the specific level.

Our specimens are flowering branches only and at a late stage, the leaves having long since fallen. The few spikelets that we have been able to dissect do show that the spikelet is 1-flowered, without any rudiment of a reduced floret above the many-nerved glumes, lemma and palea. There are clearly six anthers, which separate in the dissection and leave very thin strands of tissue which, we presume, had been loosely adnate to form a tube. Lodicules are absent and this is a state generally associated with the presence of a staminal tube (Soderstrom, 1981). The ovaries consisted of a shriveled lower section and firm crown narrowed upward into a single pubescent style and one or two stigmas. The spikelet is clearly that of a member of the Bambusinae.

The puzzling vegetative specimen collected from Bambarakelle Hill has a thick and unusual girdle at the nodes and is reminiscent of *Pseudoxytenanthera monadelpha*, but the branching is certainly different and the prominent lateral appendages of the culm leaves are unique among Sri Lanka species. After a study of the flowering material of *Dendrocalamus cinctus*, a re-examination of the perplexing vegetative collection convinced us that the two were conspecific. This is based on the type of branching, the presence of the same kind of girdle at the node, and the presence of a fine powder that covers the inner walls. The vegetative plant that was collected in December 1969 (*Soderstrom and Kulatange 1764*) was young, perhaps only a few years old, and thus coming from a recent flowering of the species. The old flowering branches were gathered in September 1972. Since flowering in bamboos usually occurs over a several-year period, some plants of the new species may have come into flower in the mid-1960s and from this resulted plants such as the one we collected at Bambarakelle Hill. A vegetative specimen at PDA (*Jayasuriya 1064*), consisting of two nodes, the included internode, and some branches and leaves, belongs to the species, and doubtless represents a young plant that resulted from the recent flowering. This specimen matches *Soderstrom and Kulatunge 1764* in the girdle, sparse appressed apically oriented brown spicules on the branch sheaths, and morphology of the foliage leaves.

ANATOMY

FIGURE 33

[NOTE.—After Soderstrom's death it was called to the attention of the second author that the description and illustration (Figure 33*a–e*) of the leaf blade transectional anatomy was atypical in being based on a very small blade (~5 mm wide) in which the section was made from near the blade apex. However, because of the unusual anatomical features in this section, including, apparently, the first report of extravascular vessel elements in the Poaceae, we are retaining the description and micrographs. It should be kept in mind however that these are in no way comparable to the transectional anatomy of the other bamboos treated in this paper. E.J.J.]

DESCRIPTION.—*Leaf blade in transverse section. Outline:* expanded and flat; symmetrical about the median vascular bundle (Figure 33*a*); relatively narrow (~7.5 μm wide) and thin (~150 μm thick) but noticeably thicker in region of the margin (~280 μm thick) (Figure 33*b*). *Ribs and furrows:* slight adaxial and abaxial ribs and furrows present (Figure 33*b*); abaxial ribs better developed than adaxial ones, particularly those opposite the first order bundles (Figure 33*c*). *Midrib:* consists of median vascular bundle only; structurally indistinguishable from all other first order bundles (Figure 33*a*). *Vascular bundle arrangement:* 15 first order vascular bundles in blade (including median bundle); in central part of blade 3 minor bundles (1 second order and 2 third order vascular bundles) situated between consecutive first order bundles (Figure 33*a*) but laterally only 1 or 2 third order bundles separate successive first order vascular bundles (Figure 33*b*). All bundles located in the middle of the blade except laterally

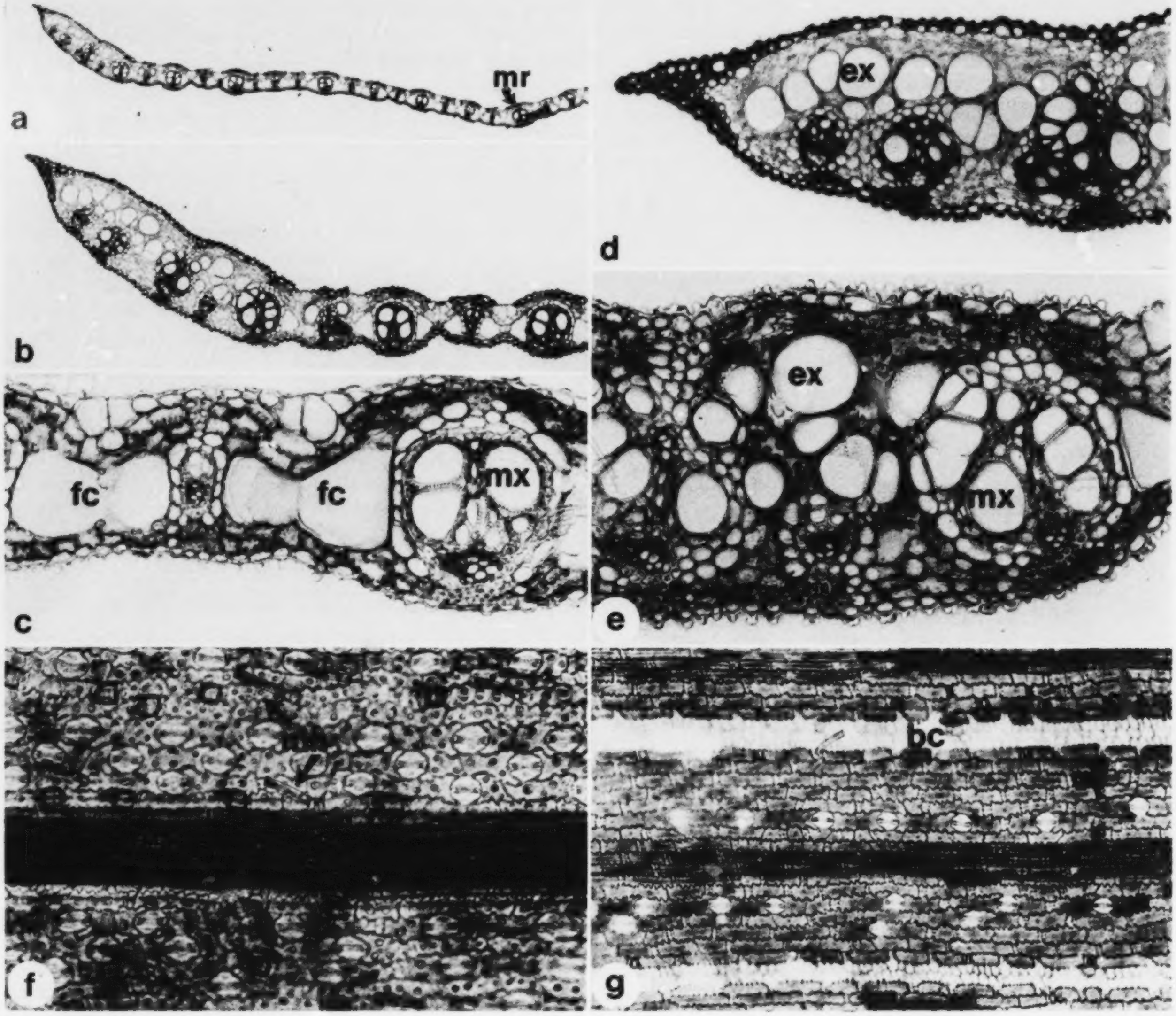

FIGURE 33.—Leaf anatomy of *Dendrocalamus cinctus* R.B. Majumder ex Soderstrom & Ellis, new species (see note under "Anatomy," this section): *a*, outline of one-half of lamina from the median vascular bundle (mr) to the margin (×23); *b*, expanded, thicker lateral part of lamina in region of margin (×58); *c*, detail of midlamina showing well-developed fusoid cavities (fc) and normal vascular bundle with a double bundle sheath and metaxylem vessels (mx) (×230); *d*, expanded leaf margin with unlignified extra-vascular vessel elements (ex) (×145); *e*, detail of lamina margin showing pitting in the extra-vascular vessel elements (ex) and normal metaxylem vessels (mx) of the first order bundles (×230); *f*, abaxial epidermis with costal (cz) and intercostal zones and microhairs (mx) (×230); *g*, adaxial epidermis with rows of bulliform cells (bc) in center of intercostal zones and with cells of costal zones (cz) similar to those of intercostal zones (×145). (Based on *Soderstrom & Kulatunge 1764*.)

where the bundles are positioned closer to the abaxial surface (Figure 33*b*). *Vascular bundle description:* third order bundles tall and narrow with vertical sides but first order bundles circular or round (Figure 33*c*). Lysigenous cavities present but no protoxylem vessels observed (Figure 33*c*). Metaxylem vessels with extremely wide diameters, often overlapping and thus appearing paired in section. *Vascular bundle sheaths:* double, even in relatively small third order bundles (Figure 33*c*); tall and narrow in third order bundle but rounded in second and first order bundles. Outer sheath of first order bundles with slight adaxial interruption and wider ab[illegible] interruption (Figure 33*c*); no bundle sheath extensions except the expanded region of the margin where irregular adaxial, arenchymatous extensions may be present (Figure 33*e*). Outer undle sheath cells elliptical to kidney-shaped, often irregular size; considerably smaller than the mesophyll cells, but with icker walls; chloroplasts lacking completely. Inner sheath ntire; consisting of single layer of cells only; cells with niformly but heavily thickened walls (Figure 33*c*). *Scler- nchyma:* adaxial and abaxial girders associated with all ascular bundles (Figure 33*b,c*); trapezoidal, narrowing to- ards bundles (particularly the adaxial girders) and more assive in association with first order vascular bundles. No clerenchyma between vascular bundles. Small, projecting ointed sclerenchyma cap at margin (Figure 33*d*). *Chlorenchyma:* rm and fusoid cells conspicuous in central part of blade Figure 33*c*) but not in expanded margin (Figure 33*e*); nvaginations of equal length and from all walls of arm cells; not vertically projecting; fusoid cell cavities present on either side of all vascular bundles except the lateral bundles situated in the thickened margin (Figure 33*b*); fusoid cavities often not separated by columns of chlorenchyma but fused with adjoining fusoid cavity (Figure 33*c*). *Colorless cells:* absent; large cells present in the expanded lateral parts of the blade (Figure 33*d*) not parenchyma but appear to be vessel elements located outside the vascular bundles; it is significant that these cells are not lignified as evidenced by non-staining with safranin (Figure 33*d*) but they possess definite alternately arranged pits (Figure 33*e*). *Adaxial epidermis:* bulliform cell groups small, fan-shaped (Figure 33*c*) and absent from lateral part of blade (Figure 33b). Outer walls of epidermal cells covered by a thick cuticle (Figure 33*d*); no prickles or macrohairs and papillae only present in region of leaf margin. *Abaxial epidermis:* no bulliform cells; each epidermal cell with individually thickened cuticle projecting into thickened cuticular papillae (Figure 33*c,e*); more than 1 papillus per cell; no macrohairs of prickles seen.

Abaxial epidermis (Figure 33*f*). *Intercostal long cells:* slightly elongated, anticlinal horizontal walls generally parallel; end walls vertical; unthickened; moderately undulating. Cell size and shape constant throughout intercostal zones. Hooks, microhairs and stomata occur between successive long cells. *Stomata:* low dome-shaped; not overarched by papillae. resent in all intercostal files throughout intercostal zones. wo adjoining interstomatal long cells usually present between uccessive stomata in any given long cell file. *Intercostal short ells:* solitary, unsilicified, tall and narrow to square with mooth outline, rare throughout epidermis and usually are only ases for microhairs and hooks. *Papillae:* small, thickened uticular papillae on all intercostal and costal long cells; many er cell; irregularly arranged with a tendency for there to be a ngle row on normal long cells and two rows on interstomatal long cells; do not overarch the stomata; and subsidiary cells without papillae. *Prickle hairs:* absent. *Hooks:* common throughout epidermis, in both costal and intercostal zones; diameter of bases less than half that of stomata; barbs very short and not conspicuous. *Microhairs:* bicellular; basal cell about 2× as long as distal cell; both cells noticeably elongated; large and conspicuous, about 3× the length of the stomata; wall of distal cell thinner than wall of basal cell and often not visible, collapsed or deciduous. Base not constricted and emerges straight from short cell. Most numerous in center and on edges of intercostal zones. *Macrohairs:* none seen. *Silica bodies:* tall and narrow with smooth outline. Not conspicuous and costal distribution irregular but usually associated with a cork cell. No granules seen. Same width as costal long cells. *Costal cells:* all files of similar composition with long cells alternating with silico-suberose couples. About 7 files comprise costal zones associated with first order bundles and 3–5 files associated with second and third order vascular bundles.

Adaxial epidermis (Figure 33*g*). *Intercostal long cells:* length about 2× width; side walls parallel; end walls vertical or angled; slightly thickened; moderately undulating. Cell size and shape constant throughout intercostal zones except in center of zones where bulliform cells occur. Silico-suberose couples between most long cells. Bulliform cell rows consist of 2–3 files of small, rounded, colorless, thin-walled cells in the center of the intercostal zones as seen in surface view. *Stomata:* low, dome-shaped, not associated with papillae. Distribution sparse and irregular; usually one row between costal zone and bulliform cell file. Separated by two or more interstomatal long cells. *Intercostal short cells:* cork-silica cell pairs located between most intercostal long cells; silica cells small, elongated with crenate outline closely enfolded by and associated with large cork cell. *Papillae:* absent, except in region of margin (Figure 33*d*). *Prickles:* absent. *Hooks:* absent, except close to margin (Figure 33*e*). *Microhairs:* bicellular, basal cell twice as long as distal cell, both cells elongated; rare and only present on intercostal long cell files adjacent to bulliform cell files. *Macrohairs:* none seen. *Silica bodies:* tall and narrow costal bodies with smooth outlines and associated with tall and narrow cork cells; intercostal silica bodies small and crenate much narrower than adjacent long cells. *Costal cells:* long cells slightly longer than intercostal long cells but slightly narrower; alternate with cork-silica cell pairs. Costal zones from 3–4 cell files wide.

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1764;* Sri Lanka, US vial no. 2570.

DISCUSSION (see note under "Anatomy").—*Dendrocalamus cinctus* is a species with peculiar leaf anatomy that differs in several significant respects from that of all other bamboo taxa investigated.

1. *Leaf outline:* The leaf is symmetrical with the lamina on either side of the median vascular bundle being identical, as are the two margins.

2. *Leaf margins:* The expanded, lateral parts of the lamina are unique as are the unlignified extra-vascular vessel elements found in this part of the blade; the small, projecting, pointed sclerenchyma cap at the leaf margin is also most unusual.

3. *Midrib:* The median vascular bundle is structurally indistinguishable from the lateral first order bundles and is not embedded in sclerenchyma tissue (all other woody bamboos

have well-defined midribs, or if the vascular system is simple, the median bundle is well supported by sclerenchyma).

4. *Vascular bundle arrangement:* The arrangement of 3 minor vascular bundles (1 second order and 2 third order) between consecutive first order bundles is unusual in the Bambusinae, which typically have 5-9 third order bundles separating successive first order bundles.

5. *Vascular bundle sheaths:* The disjointed, irregular nature of the outer bundle sheaths of the vascular bundles located in the margin is very peculiar, and would appear to be a development associated with the extra-vascular vessel elements present in this region of the leaf. These vessels appear to diverge from the normal metaxylem vessels and disrupt the outer bundle sheath at this point of divergence.

6. *Vascular bundle structure:* The extra-vascular vessel elements located in the region of the margin are of particular interest, in that they apparently diverge from the metaxylem vessels but are not lignified once outside the vascular bundles proper, although distinct pits are still evident in their side walls.

7. *Fusoid cells:* The fusoid cell cavities in the central part of the leaf lamina of *D. cinctus* are large, well developed, and often in direct contact with the adjacent cavity. This unusual fusion of adjacent fusoid cell cavities is also known in the bambusinoid species *Dendrocalamus giganteus* Munro. In contrast, in the expanded lateral part of the blade associated with the margin, fusoid cells are also present but they are very irregularly arranged, with many large air spaces being present.

8. *Arm cells:* The transectional area of the leaf occupied by arm cells is considerably reduced due to the fusion and enlargement of the fusoid cavities. Consequently, there are only two layers of arm cells present on the adaxial side of the fusoid cells, and these do not have conspicuous vertically projecting invaginations as is normal for members of the Bambusinae.

9. *Adaxial epidermis:* The expanded lateral parts of the blade are covered by a thick, papillate epidermis, whereas the central part of the lamina has a thinner, continuous cuticle without papillae. The central part of the lamina resembles the Bambusinae in this respect but the papillate lateral parts of the blade are anomalous.

Many aspects of the leaf anatomy of *D. cinctus*, therefore, differ substantially from the other members of the Bambusinae or even Bambuseae. These anatomical modifications undoubtedly result from environmental selection pressures and *D. cinctus* probably inhabits a niche which is unique for these tall, woody bamboos. It appears as if the leaf of *D. cinctus* is structured so as to increase water transport and the expanded leaf margin may function in guttation.

The anatomical justification for including *D. cinctus* within the Bambusinae depends on features of the leaf epidermis such as the non-refractive abaxial papillae overarching the stomata, elongate rod-like microhairs, and vertically elongated, tall, saddle-shaped silica bodies.

Pseudoxytenanthera Soderstrom & Ellis, new genus

Bambusa lignosa, rhizomatibus sympodialibus, caespites densos formans. *Culmi* dispersi, laxe caespitosi, ad apicem tenues et flagellares, arcuati. *Folia culmi* a cingulo incrassato abscissa. *Ramificatio:* axes secondarii cum germinatione praecoci et ramis brevibus procreantibus, axe primario dormienti vel flagellescenti ramis usque ad plures metra longis. *Folia ramorum* breviter pseudopetiolata, non manifeste tesselata. *Inflorescentia* iterauctans, pseudospiculis fasciculos capitates formatibus. *Pseudospiculae* cum duobus glumis vacuis et flosculis 1-3; glumae 10-11-nervatae; lemma 13-16 nervatum; palea 7-nervata; lodiculae 0; stamina 6, cum filamentis liberis; antherae penicillatae; ovarium glabrum stylus longus, pubescens; stigmata 3. *Fructus* caryopsis pericarpio a semine infra separabili.

TYPE SPECIES.—*Pseudoxytenanthera monadelpha* (Thwaites) Soderstrom & Ellis, new combination. Basionym: *Dendrocalamus monadelphus* Thwaites, 1864:376.

DIAGNOSIS.—Perennial grass with sympodial rhizomes. *Culms* spaced, forming loose clumps, becoming thin and whip-like at the tip and bending over. *Culm leaves* abscissile from a thickened girdle. *Branching:* secondary axes germinating precociously and producing short branches, the primary axis remaining dormant or becoming a long, whip-like branch up to several meters long. *Branch leaves* short-pseudopetiolate, not manifestly tesselate. *Inflorescences* iterauctant, the pseudospikelets forming capitate clusters. *Pseudospikelets* with 2 empty glumes and 1-3 florets; glumes 10-11-nerved; lemma 13-16-nerved; palea 7-nerved; lodicules 0; stamens 6, the filaments free, the anthers penicillate; ovary glabrous, the style long, hairy; stigmas 3. *Fruit* a caryopsis, with the pericarp separable from the seed below.

DISTRIBUTION.—A monotypic genus endemic to southern India and Sri Lanka.

10. *Pseudoxytenanthera monadelpha* (Thwaites) Soderstrom & Ellis, new combination

Dendrocalamus monadelphus Thwaites, 1864:376 [type: Sri Lanka, Ambagamuwa, Dec 1854, *C.P. 3359*, lectotype, PDA].

Oxytenanthera thwaitesii Munro, 1868:129–130.—Beddome, 1873:232, pl 322.—Gamble, 1896:72–74, pl. 64.—Gamble in Hooker, 1896:402.—Hooker f. in Trimen, 1900:316.—Camus, 1913:147.

Oxytenanthera monadelpha (Thwaites) Alston, 1931:342.—Senaratna, 1956:2

Oxytenathera densa E.-G. Camus, 1913:147 [nomen nudum].

MORPHOLOGY

FIGURES 34–36

DESCRIPTION.—Plants of more or less pluricespitose habit from shallow, sympodial pachymorph rhizomes, the culms spaced and not forming dense clumps, the culms at first stout and erect but becoming thin and whip-like at the tip and bending far over. *Culms* soft, up to 8 m tall, 1–1.5 cm diam.

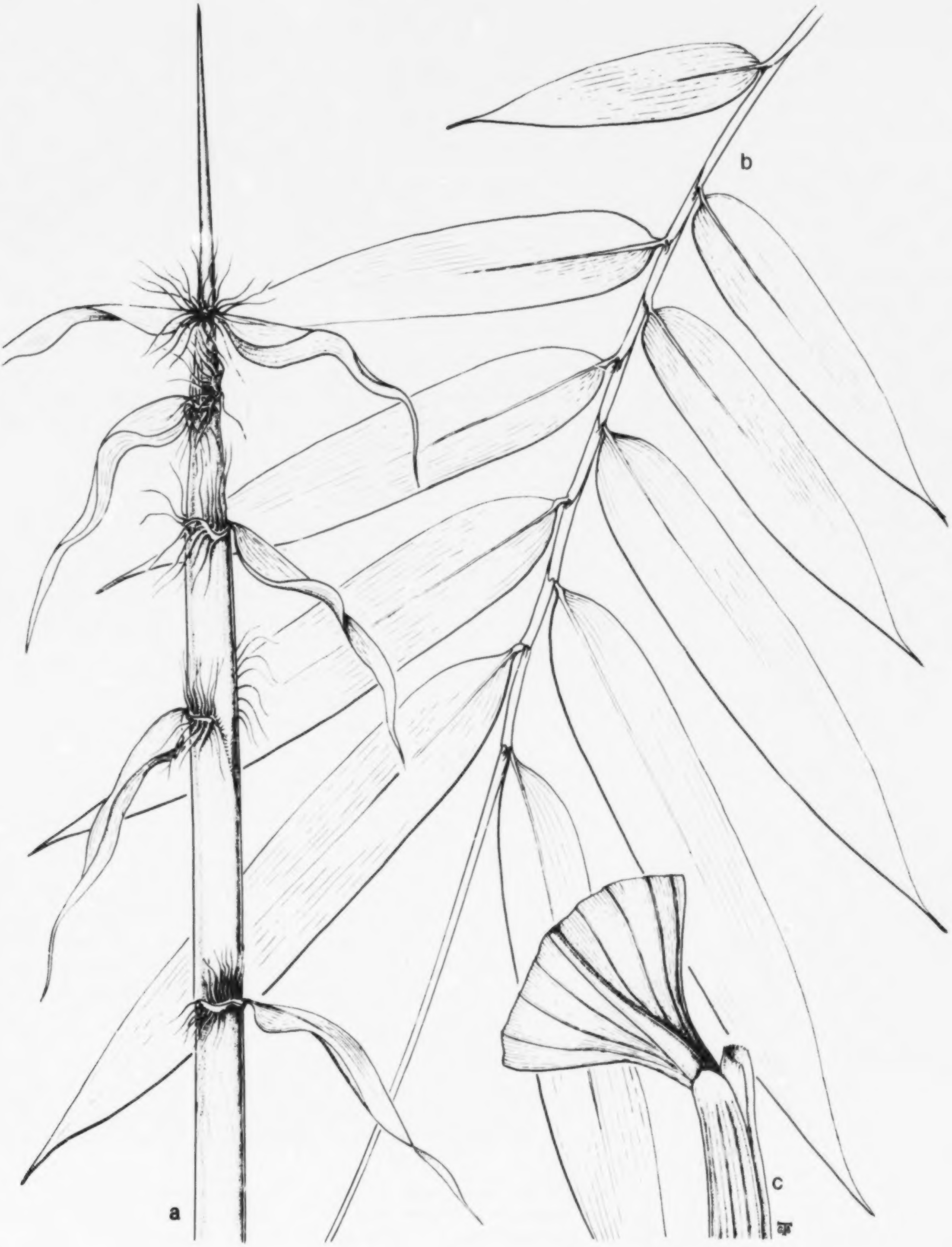

FIGURE 34.—*Pseudoxytenanthera monadelpha: a*, young shoot (×0.6); *b*, leaf complement (×0.6); *c*, base of blade (attachment to sheath), showing ligule (×3.6). (Based on *Soderstrom & Kulatunge 1605*.)

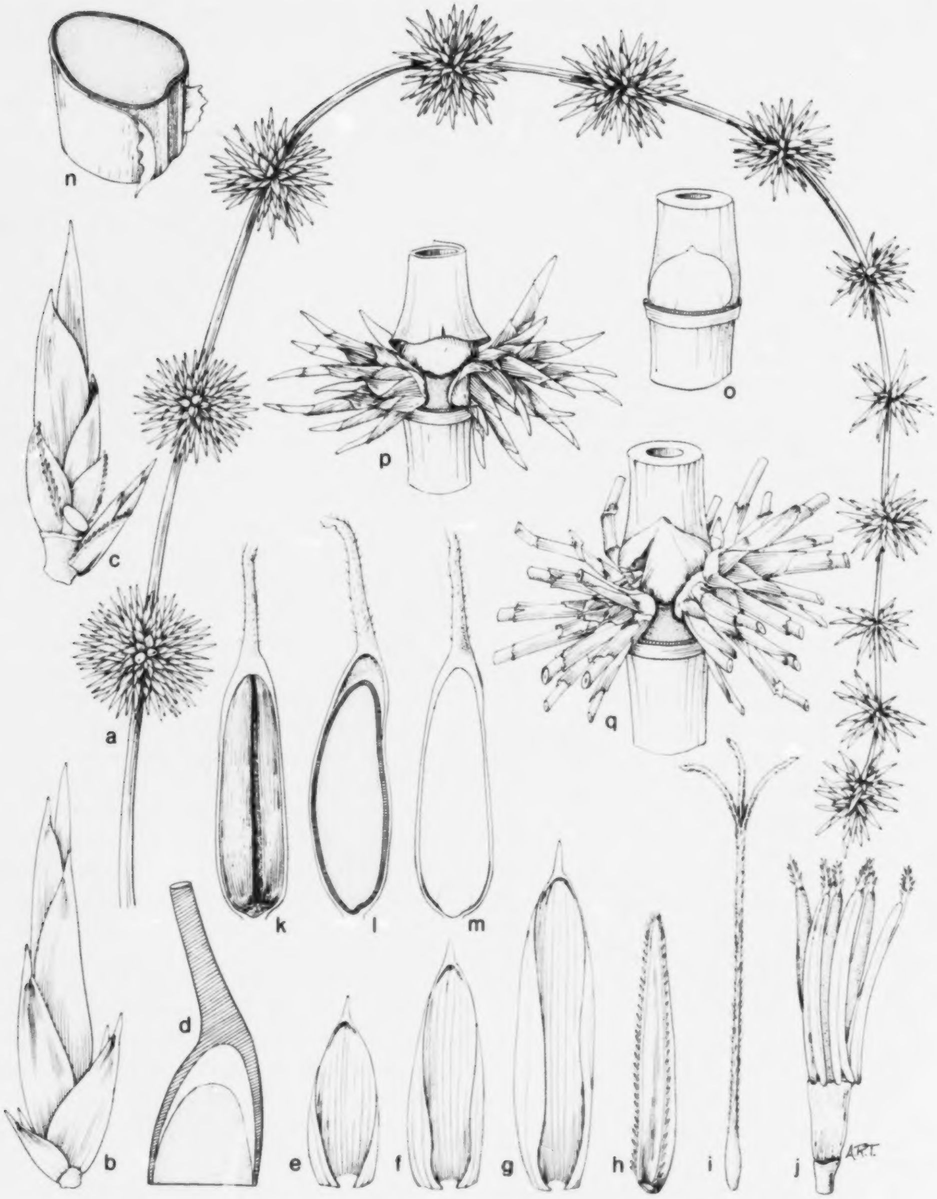

FIGURE 35.—*Pseudoxytenanthera monadelpha*: *a*, flowering branch with clusters of pseudospikelets (×0.5); *b*, pseudospikelet, with each scale at the base subtending a spikelet bud (×4.5); *c*, pseudospikelet, the new spikelet at right with 1-keeled prophyllum (×9); *d*, crown of fruit and base of persistent style, showing hollow space between seed and solid style (enlargement of upper part of *l*) (×13); *e*, 1st empty glume (×4.5); *f*, 2nd empty glume (×4.5); *g*, lemma (×4.5); *h*, palea (×4.5); *i*, young gynecium, showing hairy style and stigmas (×9); *j*, andrecium, showing fused filaments of the 6 penicillate stamens (×9); *k*–*m*, mature fruit (×9); *k*, seed within pericarp, ventral view, showing long broad hilum; *l*, lateral view of fruit, showing hollow cavity between seed and style; *m*, seed, dorsal view, showing small embryo at base; *n*, wet fruit, showing pericarp, which has separated easily from the endosperm; the broad dark band is the hilum (×13); *o*, branch bud partially subtended by thickened basal ring of sheath (×1); *p*, new branches emerging (×1); *q*, branch complement (×1). (All illustrations based on *C. P. 3359* except *o*–*q*, based on *Soderstrom 2540*.)

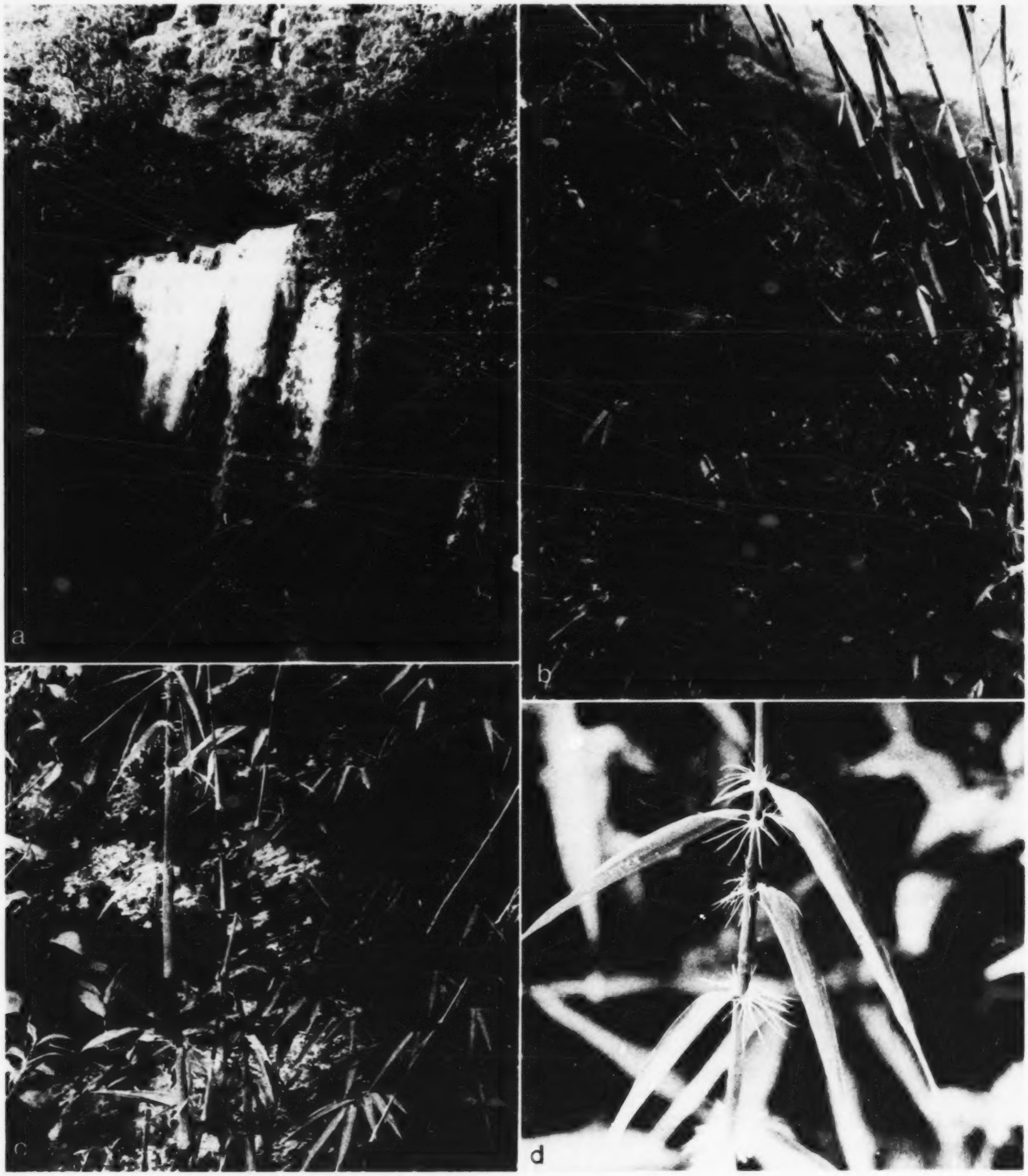

FIGURE 36.—Field photographs of *Pseudoxytenanthera monadelpha*, Nuwara Eliya District: *a*, habitat among rocks at edge of river at top of waterfall; *b*, culms at all stages of development, to the right new ones showing the culm leaves with reflexed sheaths (in a few cases the branches are beginning to emerge, extravaginally, through the base of the sheath), to the left older clusters of branches that have broken through the sheath; *c*, new culms; *d*, detail of new culm, showing the prominent and characteristic oral setae. (All photographs show *Soderstrom & Kulatunge 1644* except *a*, which is habitat of *Soderstrom & Kulatunge 1605*.)

(~2.5 cm diam., teste Senaratna), the walls relatively thick, branching from all of the nodes except the very lowest. *Culm leaves* purplish green when young, becoming stramineous, conspicuous by the dense oral setae, becoming fully developed leaves at the upper part of the culm (these lanceolate, to 25 cm long, 4 cm wide): sheath hard, brittle, pushed off by the emerging branches, abscissile from a thickened persistent band (girdle), the lower part covering the bud, smooth, glossy, sheath densely ciliate with white hairs along the upper margins, bearing dark auricles (lateral appendages) with prominent oral setae; blade deciduous, foliose, horizontal or reflexed, ovoid-lanceolate, narrowed to a truncate base, about the same length as the sheath, 10–15 cm long, 1.5–2 cm wide, green, both surfaces glabrous, the lower weakly tessellate; outer ligule lacking; inner ligule a short membranous rim from which emanate abundant and prominent oral setae up to 2 cm long. *Nodes* containing a single broadly ovoid to roundish bud with a glabrous prophyllum covered at the base by the girdle. *Branching:* secondary axes germinating precociously and producing clusters of short branches that push away the sheath or break through it at the base (girdle), the primary axis remaining dormant in bud stage or germinating to produce a new culm (if at lowermost nodes) or long whip-like branch to several meters long (if at upper nodes). *Branch leaves* in complements 27–55 cm long, 20–36 cm wide, with 7–12 leaves; blades glabrous on both surfaces, linear-lanceolate, narrowing to an acuminate tip, 12–20 cm long, 2–3 cm wide, dull green with a midvein on the upper surface conspicuous only toward the base, the lateral veins not manifest, the midvein and lateral veins on the lower surface manifest, tessellation not manifest; outer ligule a stramineous, hard ridge less than 1 mm long on one side of the petiole, ciliolate on the upper margin; inner ligule a hard ridge 1.3–1.7 mm long with a curved denticulate margin, glabrous on both surfaces. *Inflorescences* developing by way of pseudospikelets, at first terminating leafy branches. *Pseudospikelets* sessile, 13–16 mm long, narrowly obovate, subtended by a broadly triangular bract ~1/3 the length of the pseudospikelet; *prophyllum* thin, 1.5–2 mm long, 1-keeled, ciliate on the keel, triangular, followed by a single glabrous empty bract, thicker than the prophyllum, with a few faint nerves; *gemmiferous bracts* 2, broadly obtuse, 4–7-nerved, glabrous, each containing a spikelet bud, these followed by an empty bract, the first member of the spikelet proper; *branching* determinate, with the uppermost spikelet maturing first and those from the lower gemmiferous bracts later; *disarticulation* below the lower glume and the spikelet, the spikelet falling entire. *Spikelets* obovate-lanceolate, 10–12 mm long, consisting of 2 empty glumes and 1–3 florets, the lowermost developing first and strongest with reduction upwards; *glumes* 6–9 mm long, the upper longer, obovate-triangular, becoming thickened toward the pointed tip, ciliate along the middle and upper margins, otherwise glabrous, 10- or 11-nerved; *lemma* ~10 mm long, obovate-triangular, becoming thickened toward the apex, more or less glabrous throughout, 13–16-nerved with transverse veinlets; *palea* thin, a little shorter than the lemma, 2-keeled with 3 nerves between the *keels* and one on each flank, with transverse veinlets, ciliate on the keels and at the summit, otherwise glabrous, neither keeled nor ciliate (except at the apex) in the uppermost floret or single floret when spikelet 1-flowered; *lodicules* 0; *andrecium–stamens* 6, the filaments fused, anthers orange, ~3 mm long, prominently penicillate; *gynecium–ovary* glabrous, fusiform with a thickened knob-like summit narrowing into a long hairy style, remaining entire or divided into 2 or 3 stigmas; ovary wall thin, papyraceous, at summit forming a hollow crown topping the seed. *Fruit* a caryopsis, ~5 mm long, plano-convex, more or less fusiform, purplish below where the pericarp thin and easily separable from the seed, stramineous above where the pericarp thick and non-separable from the seed, forming a crown with the thickened glabrous base of the more or less persistent style; seed purplish, fusiform, with a dark brown, broad, hilum extending almost the entire length; embryo small, round, 1/8 (?) the length of the seed.

DISTRIBUTION.—Endemic to southern India and the mountains of south-central Sri Lanka.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Apr 1887, *Ferguson s.n.* (PDA); Hantane, above Wariagalla, Oct 1888, *Ridley s.n.* (PDA); Hantane, 25 Feb 1926, "408," *s. coll.* (PDA). BADULLA DISTRICT: Haputale, 24 May 1906, *"A.M.S." s.n.* (PDA). NUWARA ELIYA DISTRICT: Hakgale, Sep 1885, *Ferguson s.n.* (PDA); ~12 miles [19 km] SE of Nuwara Eliya toward Boralanda, *Gould 13352* (PDA, US); road from Kandy to Nuwara Eliya, near Ramboda, *Soderstrom & Kulatunge 1605* (PDA, US); road between Nuwara Eliya and Ramboda, *Soderstrom & Kulatunge 1644* (PDA, US); Ambagamuwa, Dec 1854, *s. coll., C. P. 3359* (PDA, lectotype); Maturata, *s. coll.* (PDA); Nuwara Eliya, Feb 1857, *s. coll., C. P. 3359* (PDA); Rangala Hill, Sep 1888, *s. coll.* (PDA). LOCALITY UNKNOWN: "Ceylon leg. Thwaites" stamped on label, *C. P. 3359* (US, 3 sheets ex W).

DISCUSSION.—Thwaites, in his original description of the species, cites *C. P. 3359*. This number consists of several sheets at PDA and at other herbaria and, as we know with the C.P. numbers, may contain gatherings by more than one collector. We have selected as lectotype a sheet at PDA represented by a branch with large leaves and a terminal inflorescence. On the sheet is written in pencil in the upper right-hand corner "C.P. 3359" and lower down, a hardly legible pencil note, "Ambagamuwa Dec 1854." We are selecting this sheet as the lectotype, as the locality is identified and Thwaites would have seen this early specimen, which bears the earliest date of the collections. There is a second collection that matches the lectotype in morphology and also in the inked identification at the lower left side of the sheet. Besides the penciled locality and Ambagamuwa, several others were written in, probably at a later date. Our description of the inflorescence is based on *C. P. 3359*.

In treating this species as a member of *Oxytenanthera*, Munro (1868) stated that he was unwilling to use the specific epithet of *"monadelphus"* and so he used instead the name *"thwaitesii,"* and this was employed by all botanists until the publication of Alston in 1931. E.-G. Camus (1913:147) lists a variety *densa* with groups of spikelets very close together, lemma with long cilia on the border and nerves manifest only at the summit. The variety is illustrated on his plate 91, figure C, where it is labeled *"O. densa,"* as if it were a species. Camus lists no specimen as the type.

The spikelets in capitate clusters, elongate, pubescent style, 6 stamens, and lack of lodicules allies this species to *Dendrocalamus*, but the unique branching pattern and vine-like nature of the culms sets it apart: the large central bud remains dormant with simultaneous production of numerous basal branches, the whole breaking through the hard sheath or pushing it off during its development. When it does develop, the large central bud becomes an elongate and whip-like branch, producing clusters of branches at each of its nodes. The hairy anther tips are characteristic of *Dendrocalamus*, *Gigantochloa* Kurz, and some species of *Bambusa*, as is the pseudospikelet and fruit with a thin pericarp below, which is separable from the seed and thickened above. The species is unlike *Bambusa* in its capitate inflorescence and non-disarticulating spikelets with short rachilla segments. We are recognizing this taxon as a distinct genus, confined to southern India and Sri Lanka, mirroring the distribution of the genus *Ochlandra*. The new genus resembles *Oxytenanthera* to some degree but Holttum (1956b) restricts that genus to the single African species, *O. abyssinica* (A. Richard) Munro, which has large pseudospikelets arranged in tufts. The hollow style is unlike that found in Asiatic species of *Oxytenanthera*, all of which Holttum would reassign to *Bambusa* or *Dendrocalamus*.

ANATOMY

FIGURE 37

DESCRIPTION.—*Leaf anatomy in transverse section. Leaf outline:* expanded and flat; asymmetrical about the midrib (Figure 37*b*) and with one margin tapering to a point (Figure 37*c*), whereas the other is rounded and abrupt. Leaf thickness ~100 µm. *Ribs and furrows:* no noteworthy undulations associated with the vascular bundles midway between the midrib and margin (Figure 37*d*); slight to medium, rounded adaxial ribs developed in association with the first 4 or 5 vascular bundles located immediately to one side of the midrib and also in conjunction with lateral 4 vascular bundles on the same side of the lamina. *Midrib:* abaxially projecting, asymmetrical structure with complex vasculature (Figure 37*b*); single large first order vascular bundle associated with 5 small bundles embedded in sclerenchyma tissue; two of these minor bundles located above the first order bundle immediately below the adaxial epidermis. *Vascular bundle arrangement:* 19 first order bundles in leaf section (including the median vascular bundle); no second order bundles present; 7–9 third order bundles separate successive first order bundles (Figure 37*a*). All bundles located slightly closer to the abaxial surface (Figure 37*d*). *Vascular bundle description:* third order bundles rounded to elliptical; xylem and phloem tissue distinguishable (Figure 37*d*); first order bundles round; protoxylem elements and lysigenous cavity present; metaxylem vessel elements wide, circular and thin-walled. *Vascular bundle sheaths:* outer sheath round, entire around third order bundles but with slight adaxial and wide abaxial interruptions in the outer sheath around the first order bundles (Figure 37*d*); parenchyma sheath cells tend to be elliptical, rather small but variable in size, with unthickened walls and lacking chloroplasts. Inner bundle sheath entire; single in third order bundles but comprising 2–3 layers in the first order bundles (Figure 37*d*); cells with heavily but uniformly thickened walls. *Sclerenchyma:* adaxial girders narrow (only 2 cells wide); abaxial girders wide (5–15 cells wide) (Figure 37*d*); no sclerenchyma present between the vascular bundles. *Chlorenchyma:* non-radiate; fusoid cavities present between all vascular bundles except in association with the lateral 6–7 bundles in the tapering margin (Figure 37*c*); fusoid cavities usually elongated, downward projecting and separated by 2 (seldom one) arm cells (Figure 37*d*). Arm cells located above the fusoid cavities with a palisade-like arrangement in three layers; invaginations vertically orientated from dorsal and ventral walls only; the layer immediately adjoining the adaxial epidermis with invaginations only from the lower wall; arm cells situated below the fusoid cavities with smaller invaginations but equally numerous from all the cell walls. *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups distinct, restricted to 3 cells per group, raised and resemble fan-shaped type; central cell largest, shield-shaped and occupies about half the leaf thickness; no cuticle developed on outer surface of bulliform cells. Outer walls of remaining epidermal cells with a continuous, distinct cuticle; no macrohairs, prickles, or papillae. *Abaxial epidermis:* no bulliform cells present; each cell with individual cuticle projected into 1 or 2 papillae; papillae narrow, cuticular (Figure 37*d*). No macrohairs or prickles.

Abaxial epidermis (Figure 37*e*). *Intercostal long cells:* elongated with length more than 3× width, parallel side walls, vertical end walls, unthickened, deeply sinuous. Cell shape varies across intercostal zones, the central cells being more elongate. No bulliform cells. Short cell pairs, or stomata, separate successive long cells. *Stomata:* shape not possible to determine due to overarching papillae; 4 rows of stomata on either side of central zone which is 5 files wide; stomatal files adjoin one another; stomata separated by single interstomatal long cell. *Intercostal short cells:* paired; cork cell tall and narrow with somewhat crenate outline; enfolding tall silica cell; present between all long cells in central files of intercostal zones; often associated with basal cell of microhairs. *Papillae:* small, thickened, cuticular; present on all long cells, including those of the costal zones; 8–12 papillae in single (sometimes double) row in center of each centrally located long cell; double rows, less regularly arranged, associated with the shorter interstomatal long cells; 4 papillae overarch each stoma.

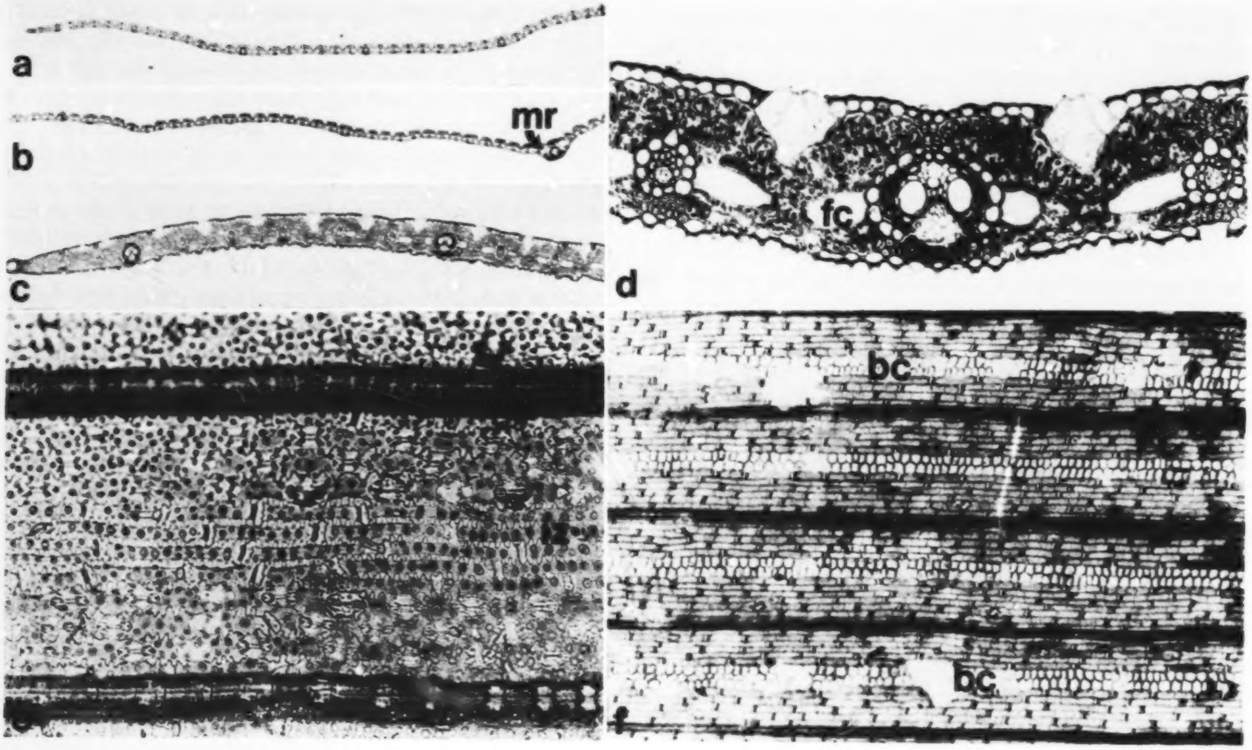

FIGURE 37.—Leaf anatomy of *Pseudoxytenanthera monadelpha: a,* outline of lateral part of lamina (×15); *b,* blade outline in region of asymmetrical midrib (mr) (×15); *c,* tapering margin and absence of ribs and furrows (×62); *d,* detail of lamina anatomy illustrating arm cell invaginations, fusoid cell cavities (fc) and double inner bundle sheath (×250); *e,* abaxial epidermis with vertically orientated silica bodies and papillate long cells in intercostal zone (iz), with these papillae overarching the stomata (×250); *f,* adaxial epidermis with bulliform cells (bc) and cork-silica cell pairs (×100). (Based on *Soderstrom & Kulatunge 1605.*)

Prickles and hooks: not present on preparation studied. *Microhairs:* narrow, elongated, rod-like; total length about double that of the stomata; distal cell thin-walled and usually not discernible. Confined to central files of intercostal zones and immediately adjacent to the costal zones. *Macrohairs:* absent. *Silica bodies:* costal bodies tall, saddle-shaped with the two ends raised in three dimensional view. Intercostal bodies much smaller, tall, and narrow, enfolded by short cork cell. *Costal cells:* silica cells alternate with short to elongate costal long cells with sinuous walls; costal zones overlying third order vascular bundles consist of 1 or 3 files of cells.

Adaxial epidermis (Figure 37*f*). *Intercostal long cells:* lateral cells elongated, rectangular with slightly sinuous walls; separated by silico-suberose couples. Central two files consist of angular bulliform cells, alternating and interlocking with one another; that only two files of bulliform cells are visible in surface view is difficult to explain when reference is made to the transverse section where three files of cells clearly constitute the bulliform groups (Figure 37*d*). *Stomata:* absent. *Intercostal short cells:* paired, with both cork and silica cell being tall and narrow; located between all long cells except the bulliform cells. *Papillae:* absent. *Prickles and hooks:* none seen. *Microhairs:* not observed. *Macrohairs:* absent. *Silica bodies:* tall and narrow in both costal and intercostal zones; associated with tall and narrow cork cell. *Costal cells:* identical to intercostal files and only distinguishable due to presence of underlying sclerenchyma tissue.

SPECIMEN EXAMINED.—*Soderstrom and Kulatunge 1605,* Sri Lanka; US vial no. 422.

DISCUSSION.—The leaf anatomy of *Pseudoxytenanthera monadelpha,* not previously discussed in the literature, conforms very closely to that of the Bambusinae, and the reader is referred to the anatomical discussion of *Bambusa vulgaris* for an anatomical diagnosis of this subtribe. The only anatomical divergences noted were that the leaf blade of *P. monadelpha* is thinner than other members of the *Bambusa* complex, the midrib is less well developed, and fusoid cells are absent from the lateral parts of the leaf.

The abaxial epidermal structure, as illustrated in Figure 37*e*, warrants comment. No hooks are visible in this preparation but Figure 37*c* illustrates many hooks in the abaxial epidermis of this section in the region of the leaf margin. It can, therefore, be expected that epidermal scrapes prepared from other parts of the leaf blade may well possess hooks.

Subtribe SCHIZOSTACHYDINAE Soderstrom & Ellis

Subtribe SCHIZOSTACHYDINAE Soderstrom and Ellis, 1987:238.

TYPE GENUS.—*Schizostachyum* Nees von Esenbeck.

DIAGNOSIS.—*Morphology:* Plants erect or uncommonly scandent or vining; branches often subequal, borne at the nodes and developing extravaginally; inflorescences iterauctant; stamens 6 to many (120); ovary glabrous, the style elongated, persistent; stigmas 3. *Leaf anatomy:* similar to the Arundinariinae and Bambusinae, but microhairs larger and with basal cell thick-walled, papillae smaller ("micropapillae") and refractive, and prickles usually absent; keel S-shaped, with complex vasculature.

DISTRIBUTION.—A subtribe of 8 genera found in lowland tropical Asia and Madagascar.

Key to the Genera and Species of the Schizostachydinae in Sri Lanka

Fruit with pericarp dry; stamens 6; stigmas plumose . . . . . . 11. ***Davidsea attenuata***
Fruit with pericarp fleshy at first; stamens 27; stigmas hispid . . . .
. . . . 12. ***Ochlandra stridula***

Davidsea Soderstrom & Ellis, new genus

Bambusa lignosa, caespites densos formans, rhizomatibus sympodialibus. *Culmi folia* supra basim dehiscentia in cingulum persistentia. *Ramificatio* intravaginalis, rami monade e ramo centrali primario dominanti et ramis secondariis duobus et ramis subsidiariis constante, ramis primariis et plerumque ramis secundariis elongatis tenuibus flagelliformibus. *Ramorum folia* breviter pseudopetiolata, non valde tesselata. *Inflorescentia* iterauctans, pseudospiculis sympodialiter evolutis. *Pseudospiculae* cum una gluma vacua et pluribus flosculis, solum infimo evoluto, infra glumas disarticulatae; glumae 13-nervatae; lemma 16-nervatum arcte convolutum; palea bicarinata; lodiculae 3; stamina 6; ovarium glabrum, in stylo compresso et 3 stigmatibus breviterplumosis attenuatum. *Fructus* ignotus.

TYPE SPECIES.—*Davidsea attenuata* (Thwaites) Soderstrom & Ellis, new combination. Basionym: *Bambusa attenuata* Thwaites, 1864:375.

DIAGNOSIS.—Perennial grass with sympodial rhizomes producing dense clumps. *Culm leaves* dehiscent above the base, leaving a girdle. *Branching* intravaginal, the branch complement consisting of a central dominant primary branch with two secondary branches and additional orders of branching to form a cluster, the primary and usually secondary branches becoming elongate, thin, and whip-like. *Foliage leaves* short-pseudopetiolate, not manifestly tesselate. *Inflorescences* iterauctant, the pseudospikelets developing sympodially. *Pseudospikelets* with one empty glume and several florets, only the lowermost developing, disarticulating below the glumes; glumes 13-nerved; lemma 16-nerved, tightly convolute; palea bikeeled; lodicules 3; stamens 6; ovary glabrous, gradually narrowed into a flat style and 3 shortly plumose stigmas. *Fruit* unknown.

DISTRIBUTION.—One species, known only from the mountains of south-central Sri Lanka.

11. *Davidsea attenuata* (Thwaites) Soderstrom & Ellis, new combination

Bambusa attenuata Thwaites, 1864:375 [type: Sri Lanka, *C.P. 3255*, lectotype, K].

Teinostachyum attenuatum (Thwaites) Munro, 1868:143–144.—Beddome, 1873:234.—Gamble, 1896:100, pl. 88.—Gamble in Hooker, 1896:410–411.—Hooker f. in Trimen, 1900:317.—Camus, 1913:163–164, pl. 92: fig. c.—Senaratna, 1956:25.

MORPHOLOGY

FIGURES 38–40

DESCRIPTION.—Plants of unicespitose habit, the rhizomes sympodial, pachymorph with a short neck 3–5 cm long, producing a dense clump with closely placed culms, the culms hard, light green with a white blush at the summit of the internode, erect below but whip-like terminally and strongly arching after branching, up to 8 or 9 m tall, 1.5–2.5 cm diam., consisting of 26–30 nodes, the lowermost two without buds, the next three with buds, these dormant, the remaining with buds that germinate more or less acropetally, those between the longest internodes having the best-developed branches; internodes cylindrical, hollow, the longest 37–38 cm long, when new bright green except toward the summit where roughened and covered with fine white hairs. *Culm leaves:* sheath when young maroon toward the summit and pale green below, becoming stramineous with age, covered with scattered appressed white hairs (spicules), thick at the base and leaving a girdle upon abscission of the sheath, strongly tessellate on the inner surface; blade tardily deciduous, horizontal to slightly reflexed, $^1/_3$–$^1/_2$ as long as the sheath, linear-lanceolate, up to 8.5 cm long, ~1 cm wide, the margins twisted toward the base, the edges of the acuminate apex inrolled and fused into a hard point, glabrous on the lower surface, the upper surface hirtellous on the intercostal zones with sparse long hairs intermixed, the long hairs becoming dense toward the apex;

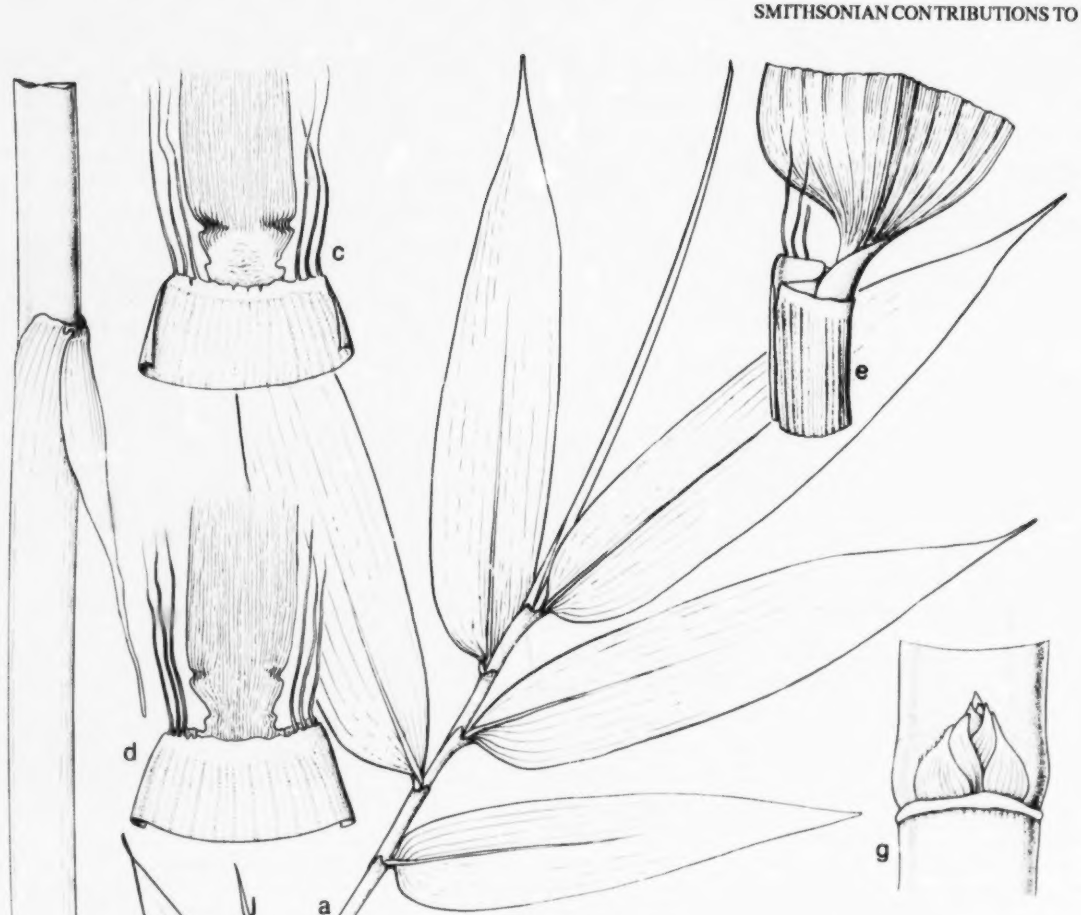

FIGURE 38.—*Davidsea attenuata: a*, leaf complement (×0.6); *b*, young culm with sheath in place (×0.6); *c*, culm sheath ligule, adaxial view (×1.2); *d*, culm sheath ligule, abaxial view (×1.2); *e*, leaf ligule (×3.5); *f*, young branch complement (×0.6); *g*, mid-culm bud (×1.2); *h*, rhizome (×0.3). (Based on *Soderstrom & Kulatunge 1657*.)

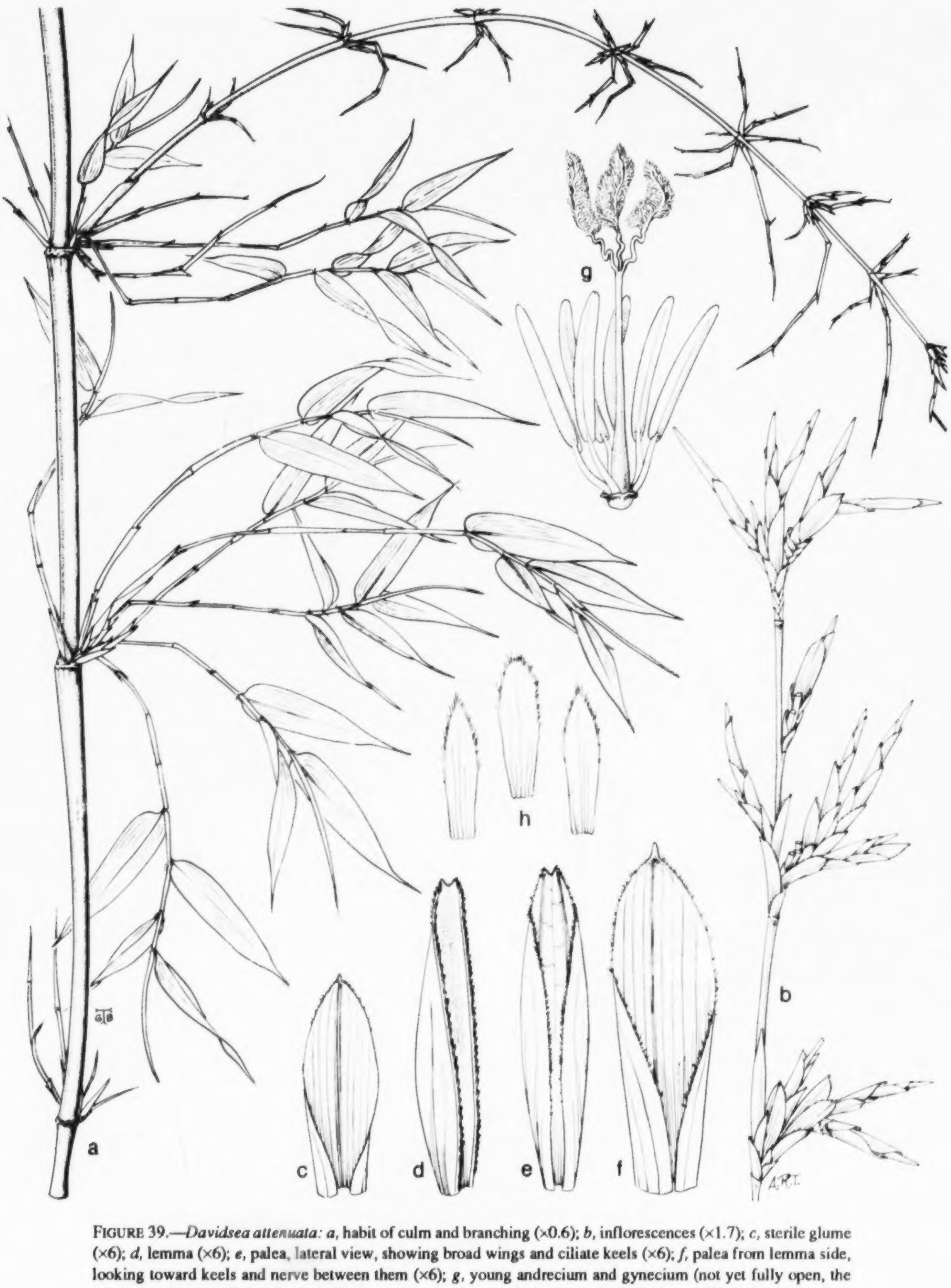

FIGURE 39.—*Davidsea attenuata: a*, habit of culm and branching (×0.6); *b*, inflorescences (×1.7); *c*, sterile glume (×6); *d*, lemma (×6); *e*, palea, lateral view, showing broad wings and ciliate keels (×6); *f*, palea from lemma side, looking toward keels and nerve between them (×6); *g*, young andrecium and gynecium (not yet fully open, the stigmas unexpanded) (×4.5); *h*, lodicules (×6). (*a* based on *Soderstrom & Kulatunge 1657; b* based on *C. P. 3255;* and *c–h* based on *Davidse & Sumithraarachchi 7968.*)

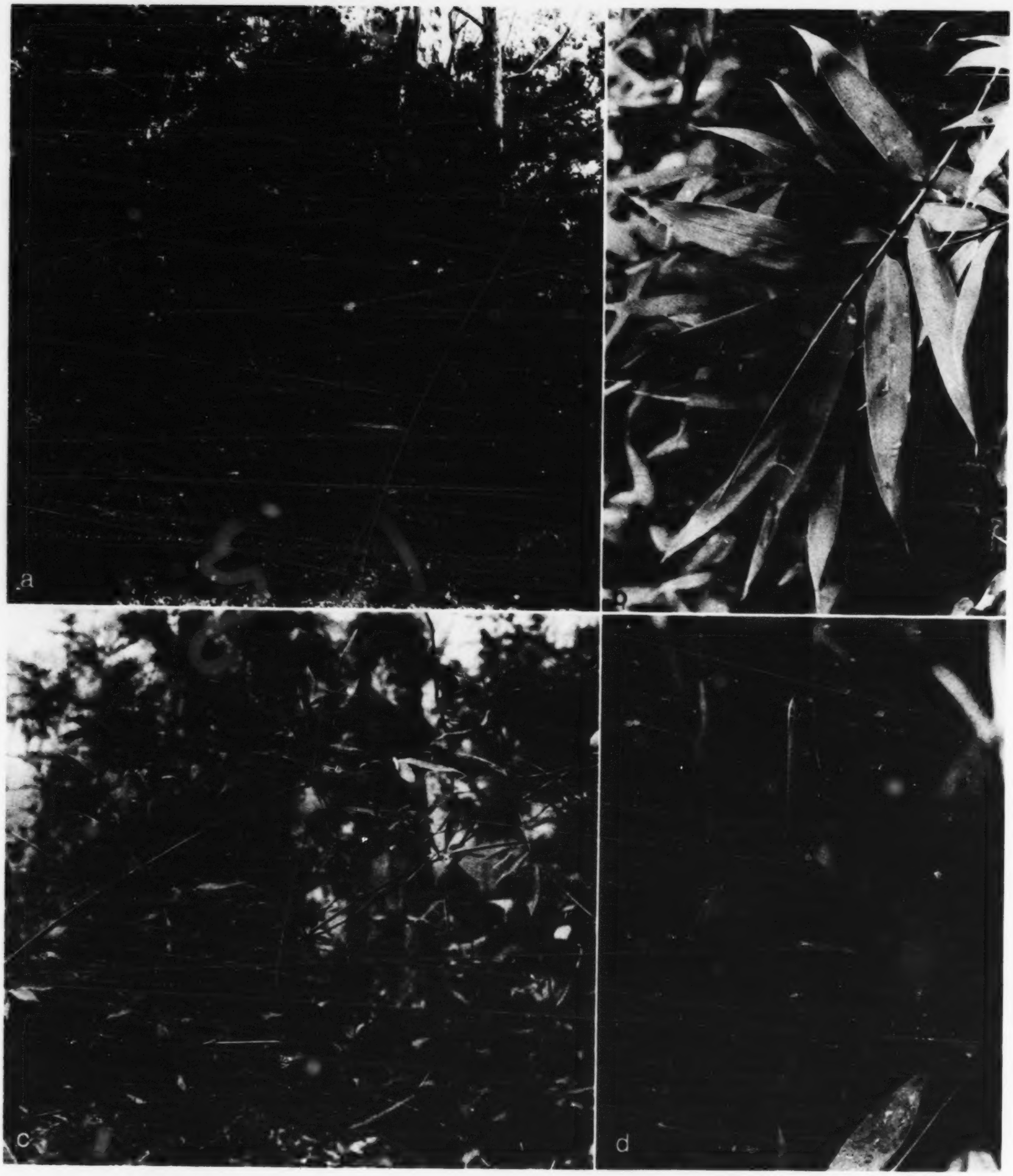

FIGURE 40.—Field photographs of *Davidsea attenuata*, in woods between Horton Plains and Ohiya, Badulla District, at 1890 m elevation: *a*, habit and habitat, showing erect new culms shooting up through vegetation; *b*, leaf complement; *c*, arching culm, showing node (arrow) from which the central branch has elongated and will climb over vegetation; *d*, new culm, showing leaf with reflexed blade. (Photographs show *Soderstrom & Kulatunge 1657*.)

inner ligule a truncate membrane ~2 mm long with a denticulate margin, glabrous on both surfaces; lateral appendages small, with a few white oral setae; outer ligule lacking. *Nodes* containing a single bud, this low, broad, more or less triangular, the prophyllum glabrous, margins sparingly ciliolate, the base covered by the thick girdle. *Branching* intravaginal: central dominant primary branch developing first, followed by two secondary branches and soon after by additional orders to form a cluster, the central branch and usually the two secondary ones becoming elongate, thin and whip-like, and arching over the other vegetation, their nodes in turn producing clusters of branches. *Foliage leaves* in complements to 40 cm long, 30 cm wide, with 9 or 10 leaves in the complement: most fully developed blades 10–20 cm long, 2–3 cm wide, lanceolate with an acuminate tip, the edges smooth or denticulate, paler green on the lower surface, glabrous on both surfaces, the mid- and lateral veins not manifest on the upper surface, midvein prominent on the lower surface and lateral veins clearly delimited, tessellation not manifest, short-petiolate and at length abscissile from the sheath; sheath glabrous except for a few appressed hairs toward the summit and cilia on the upper overlapping margin, the upper margin slightly elevated into an auricle and sometimes bearing a short lateral appendage with oral setae; inner ligule a minute truncate rim less than 1 mm long; outer ligule a hard glabrous rim less than 1 mm long. *Inflorescences* developing by way of pseudospikelets terminating leafy branches or occurring on short leafless branches clustered at the nodes; internodes of the flowering branches flat below and becoming thickened upward. *Pseudospikelets* sessile, ~2 cm long, subtended and at first covered by a firm, persistent, many-nerved, glabrous bract, ciliate on the lower margins, otherwise glabrous, followed closely by the prophyllum; *prophyllum* gemmiferous, ~8 mm long, obtuse at the apex, the 2 keels winged, ciliate, with the interkeels concave, nerveless and purberulent, the lateral flanges each with 2 or 3 nerves and glabrous; gemmiferous bracts (glumes) 2 or 3, the first 2 occurring close together, with a long internode between the 2nd and 3rd and/or the uppermost one and empty glume of the spikelet, the internodes, when long, flat below and becoming thickened upward, the bracts ciliate on the lower 3/4 of the margins, many-nerved, glabrous, the internode preceding the empty glume with a thickened ridge at its summit, clearly distinct from the base of the empty glume; branching sympodial, with only the bud directly below the spikelet developing upon maturation of the spikelet. *Spikelets* consisting of 1 empty glume and several florets, only the lowermost of which develops fully, the other one or two depauperate, followed by an empty lemma and/or a terminal empty lemma, the rachilla internodes short, 1–2 mm long, not disarticulating, the spikelet itself disarticulating below the glume; glume single, ~11 mm long, the margins ciliate on the lower 3/4, otherwise glabrous, apiculate, ~13-nerved *fertile lemma* ~14 mm long, glabrous, apiculate, firm, 16-nerved, with transverse veinlets, tighty convolute, enclosing the palea and flower; *palea* thin, shorter than the lemma, with an obtuse tip, ciliate on the 2 keels and at the summit, otherwise glabrous, with 1 nerve between the keels and 1 in each lateral flank; *lodicules* 3, obovate and pointed at the tip, the two anterior broader than the single posterior, all ~2.4 mm long, a little thickened at the base, otherwise thin, many-nerved; *andrecium–stamens* 6, the filaments free, anthers yellow, ~2 mm long, basifixed, shortly apiculate; *gynecium–ovary* glabrous, gradually narrowed into a flat style divided halfway or less into 3 shortly-plumose stigmas; *fruit* unknown.

DISTRIBUTION.—Endemic to Sri Lanka.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—KANDY DISTRICT: Knuckles Mountain, *Gould & Balakrishnan 13898* (US); Rangala Hill, east of Kandy, *Soderstrom & Kulatunge 1770* (PDA, US). BADULLA DISTRICT: between Horton Plains and Ohiya, *Soderstrom & Kulatunge 1657* (PDA,US). NUWARA ELIYA DISTRICT: ~6 miles [9 km] NW of Nuwara Eliya along the Gampola-Nuwara Eliya road, *Davidse & Sumithraarachchi 7968* (PDA, US). LOCALITY UNKNOWN: "Thwaites 1861" [probably year received at P], *s. coll., C. P. 3255* (US fragment ex P); "Thwaites 1863" [probably year received at Caen], *s. coll., C. P. 3255* (US fragment ex P[Caen]); "Ceylon" without further information, *s. coll.* (US sheet numbers 1021686, 1021687, 1021688).

DISCUSSION.—The inflorescence of this bamboo at first terminates leafy branches, the leaves replaced by firm persistent bracts, each bearing in its axil a primary pseudospikelet. The pseudospikelet, which is actually a condensed flowering branch that looks like a spikelet, is marked at its base by a prophyllum. This bears a rudimentary bud that does not develop as do the next 2 or 3 bracts, otherwise known as gemmiferous glumes. The uppermost glume is empty. It represents the first element of the spikelet proper and is clearly demarcated from the internode that supports it. When the mature spikelet falls, it is succeeded by another spikelet that develops from the bud in the axil of the glume that precedes the empty glume. When the second spikelet matures it is succeeded by another one that develops from the bud in the axil of the glume that precedes it, and so on. The branching of the pseudospikelet is thus sympodial, resulting in a series of rachis segments lined up in an elongated row after the spikelets have fallen. This condition is opposed to that of a capitate formation that is the result of monopodial development, where several buds of the pseudospikelet develop into spikelets and several buds in each of these develops further until they have all become crowded into a sphere or capitulum, as is the case in *Pseudoxytenanthera monadelpha*. The spikelet itself is many-flowered but only the lowermost one develops fully, the others remaining undeveloped. Thus, in the pseudospikelet, reduction has occurred from below upward, while in the spikelet it has been from above downward.

This species is known only from the mountains of south-central Sri Lanka. The unusual inflorescence (with sympodially developing pseudospikelets) and glabrous ovary with an elongate style show it to be distinct from *Bambusa*, and the long, whip-like branches at each node further separate it from that genus. The glabrous ovary, elongate style, and leaf epidermal anatomy are reminiscent, rather, of *Schizostachyum*, but as we understand *Schizostachyum* and genera allied to it or possibly synonymous with it (*Cephalostachyum* Munro, *Teinostachyum* Munro), the branch complement consists of numerous subequal branches that break through the sheath; in other words branching is extravaginal. The ovary, which is glabrous in these genera, extends upward into an elongate triquetrous style that is divided into 2 or 3 short stigmas. This style hardens on maturity and remains as a beak on the fruit. The Sri Lanka species long called *Teinostachyum attenuatum* (here *Davidsea attenuata*) does not conform to the schizostachyoid pattern. The branch complement consists of three primary branches that develop more or less simultaneously, followed by additional and smaller secondary branches, all developing within the sheath in an intravaginal fashion. The ovary, which is glabrous, extends into a long style that divides into three well-developed plumose stigmas. It is round and does not project from the spikelet. The type of the genus *Teinostachyum*, *T. griffithii* Munro, as far as we can tell from herbarium material and the literature, conforms to the schizostachyoid type. It is verticillately branched and, judging from the illustration that accompanies the original description, extravaginal. These features of branching exclude the Sri Lanka species, as do a number of other features, such as the 3–5 fertile florets per spikelet and the two or three very short stigmas that terminate an elongated style. Certainly the species from southern India (*T. beddomei* C.E.C. Fischer) does, for the senior author has collected ample flowering material (*Soderstrom 2545*).

The pseudospikelet with a many-flowered spikelet, 6 stamens and 3 lodicules conforms to *Bambusa* but the glabrous ovary and long style are not features of that genus. Then, too, the sympodial development of the pseudospikelets is not characteristic of that genus, nor the curious branching habit in which each of the three major branches becomes long and whip-like.

We cannot therefore maintain this taxon in *Teinostachyum* nor place it in any other genus known to us and we are establishing for it the new genus *Davidsea*, named in honor of Dr. Gerrit Davidse (born 1940, The Netherlands) of the Missouri Botanical Garden, outstanding agrostologist, unexcelled collector of grasses, and collaborator on the Flora of Ceylon Project. His excellent collection of flowering material of this taxon allowed us to interpret the nature of this bamboo.

The description of the inflorescence is based on US nos. 1021686 and 1021687, both marked Ceylon but without further information, and *Davidse & Sumithraarachchi 7968*.

ANATOMY

FIGURE 41

DESCRIPTION.—*Leaf blade in transverse section. Leaf outline:* open, expanded blade; asymmetrical about midrib (Figure 41*b*) with one margin tapering (Figure 41*a*) and the other truncated and strongly ribbed; leaf thickness ~150 µm. *Ribs and furrows:* narrow and shallow adaxial furrows present between all vascular bundles across the width of the blade; associated ribs very wide with flattened tops (Figure 41*a*). More prominent, rounded ribs located to one side of the midrib (Figure 41*b*) and with the margin on this side of the lamina. *Midrib:* abaxially projecting, broadly S-shaped, asymmetrical structure with complex vasculature (Figure 41*b*); two minor bundles located just above the central major bundle; all bundles embedded in thickened sterome tissue. *Vascular bundle arrangement:* 15 first order bundles in the blade; no second order bundles; 6–7 third order bundles separate successive first order bundles. All bundles positioned slightly towards the abaxial side (Figure 41*c*). *Vascular bundle description:* third order bundles elliptical (Figure 41*c*); first order bundles round; lysigenous cavity and protoxylem visible; metaxylem vessels wide, thin-walled and circular in shape (Figure 41*c*); phloem adjoins the inner sheath. *Vascular bundle sheaths:* double, even around third order bundles (Figure 41*c*). Outer sheath round with wide abaxial and slight adaxial interruptions; no bundle sheath extensions. Outer sheath cells rounded, inflated, with slightly thickened walls and cytoplasmic contents (Figure 41*c*); 9–12 outer sheath cells around third order bundles and up to 19 around the first order bundles. Inner sheath complete, of 1–2 layers of uniformly, but heavily thickened cells (Figure 41*c*). *Sclerenchyma:* adaxial and abaxial girders associated with all vascular bundles (Figure 41*c*); abaxial girders wide and shallow whereas adaxial girders narrow and deep, being only uni- or biseriate; no sclerenchyma present between the bundles; minute sclerenchyma cap in margin (Figure 41*a*). *Chlorenchyma:* fusoid cell cavities present on either side of all bundles; elongated, downward projecting and located nearer the lower epidermis (Figure 41*c*); adjacent fusoids separated by two chlorenchyma cells; chlorenchyma comprised of arm cells; adaxially situated arm cells with vertical invaginations from the lower cell wall but abaxial arm cells with shorter invaginations projecting inwards from all sides (Figure 41*c*). *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups fan-shaped, located at the bases of narrow, shallow furrows (Figure 41*c*); central cell large (equal to at least half the leaf thickness), shield-shaped, and associated with only one much smaller cell on either side. Outer walls of epidermal cells covered by a distinct but continuous cuticle; costal and intercostal cells equal in size and of similar shape; no epidermal appendages visible. *Abaxial epidermis:* no bulliform cells present; costal and intercostal cells of similar size and shape with the central cells of the intercostal zones being the largest (Figure 41*c*); costal and intercostal cells with prominent, often

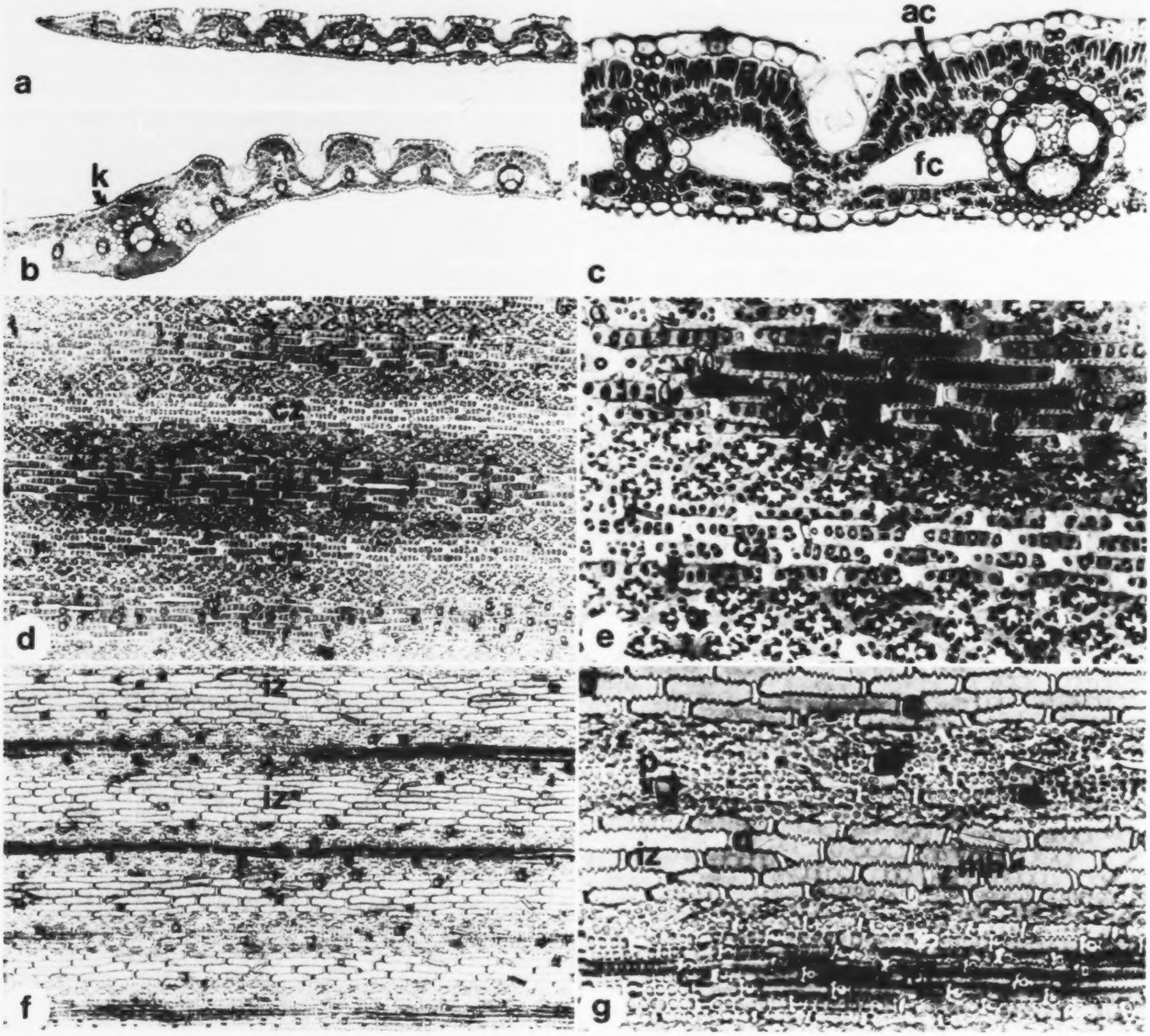

FIGURE 41.—Leaf anatomy of *Davidsea attenuata: a*, tapering margin and adaxial ribs and furrows (×58); *b*, outline of midrib (k) showing complex vasculature and asymmetrical lamina (×58); *c*, detailed anatomy with fusoid cavities (fc), vertical invaginations from lower wall of adaxially located arm cells (ac), and vascular bundle structure (×230); *d*, abaxial epidermis showing undifferentiated costal zones (cz) and intercostal zones (iz) (×93); *e*, costal files (cz) with single row of thickened papillae and asperities (p) and lateral intercostal files with papillae overarching the stomata (×230); *f*, abaxial epidermis showing intercostal zones (iz) and very narrow costal zones (×93); *g*, higher magnification showing central intercostal long cells without papillae (iz), microhairs with thickened basal cells (mh), prickles (p), and silica bodies in costal zone (cz) (×230). (Photographs *a–e* based on *Soderstrom and Kulatunge 1657; f,g* based on *Soderstrom 2554.*)

bifurcate papillae; few prickle bases present in the centers of the intercostal zone.

Abaxial epidermis. Epidermal zonation: costal and intercostal zones undifferentiated in surface view (Figure 41*d,f*); costal zones obscure and occur in centers of papillate zones (Figure 41*g*). *Intercostal long cells:* elongated, with parallel, sinuous side walls and vertical end walls. Cell shape varies across intercostal zones with the central files consisting of larger, somewhat inflated cells which may be either papillate (Figure 41*d,e*) or not (Figure 41*f,g*). Short cell pairs separate the central long cells (Figure 41*g*) and stomata the lateral ones. *Stomata:* shape completely obscured by overlapping papillae; 2-3 stomatal files on either side of each costal zone; successive stomata in a file separated by single interstomatal cells; stomatal files adjacent to one another. *Intercostal short cells:* paired; both cork and silica cell tall and narrow (Figure 41*g*); present on central files of intercostal zones only (Figure 41*e,g*); situated between all long cells in these files. *Papillae:* rather large, often with bifurcating or multiple heads; present on all epidermal long cells (both costal and intercostal) (Figure 41*d*) or absent on central files of intercostal zones (Figure 41*f*); either in single central row of up to 10 papillae on central intercostal files or somewhat irregular in arrangement on lateral files; 4-6 papillae overarch stomata (Figure 41*e*). *Prickles and hooks:* prickles with distinct barbs scattered along costal files and central files of intercostal zones (Figure 41*f,g*); these prickles may lack barbs and are then termed asperities (Figure 41*e*). *Microhairs:* finger-like; total length of hair greater than 4× the stomatal length (Figure 41*g*); basal and distal cell about equal in length but basal cell with thicker walls; these often appear silicified and contain cytoplasmic contents (Figure 41*g*); confined to either side of the files of stomata. *Macrohairs:* none seen. *Silica bodies:* may be obscured by papillae (Figure 41*e*); when visible costal bodies saddle-shaped, closely associated with a tall cork cell (Figure 41*g*); intercostal bodies tall and narrow. *Costal cells:* often obscured by papillae; elongated rectangular, alternating with silico-suberose couples (Figure 41*g*). Costal zones very narrow as seen in surface view, being only 3 cells wide.

Adaxial epidermis. Intercostal long cells: rectangular, with slightly sinuous walls; central three files consist of short, wide bulliform cells arranged in an interlocking manner. *Stomata:* absent from this surface. *Intercostal short cells:* long cells separated by tall and narrow short cells. *Papillae:* absent; single row of minute, refractive micro-papillae present on all intercostal long cells except the bulliform cells. *Prickles and hooks:* absent. *Microhairs:* appear to be absent on this surface. *Macrohairs:* absent. *Silica bodies:* tall and narrow in both costal and intercostal zones. *Costal cells:* costal zones indistinguishable in surface view and costal files (overlying the bundles) are identical to the intercostal files.

SPECIMENS EXAMINED.—*Soderstrom and Kulatunge 1657; Soderstrom 2554;* both from Sri Lanka.

DISCUSSION.—*Davidsea attenuata* possesses leaf anatomy which is typical of that of the Schizostachydinae. The larger microhairs with noticeably thick-walled basal cells and the refractive papillae of the adaxial long cells characterize this subtribe. Prickle hairs are also not common on the leaves of this group. In all these diagnostic features *D. attenuata* agrees with the diagnosis of the Schizostachydinae and the leaf anatomy fully supports its inclusion in this subtribe.

An interesting feature of the leaf anatomy is the lack of costal zone differentiation in the abaxial epidermis. This is notwithstanding the fact that well-developed abaxial sclerenchyma girders are present but, even in transverse section, it is apparent that the overlying epidermal cells are not structurally different from those not in contact with the sclerenchyma fibres. This is most unusual, particularly where the girders themselves are as wide as they are in this species. It is also unusual for epidermal cells overlying sclerenchyma girders to be papillate as is the case here. These unusual features appear to be most strongly developed in those taxa of the Schizostachydinae which possess refractive type of papillae, as is the case in *D. attenuata.*

Genus *Ochlandra* Thwaites

Ochlandra Thwaites, 1864:376.

TYPE SPECIES.—*Ochlandra stridula* Moon ex Thwaites, 1864:376.

DIAGNOSIS.—*Rhizomes* sympodial, pachymorph, without elongated necks. *Culms* in cespitose clumps, in most species weak, often not self-supporting. *Internodes* terete, hollow, thin-walled. *Nodes* more or less flat, not prominent, with or without an upper ridge. *Branch buds* solitary at each culm node, broad, positioned at the nodal line. *Branching* intravaginal. *Branch complements* at midculm nodes positioned at the nodal line, with several to many subequal branches, the primary and secondary ones weakly to strongly dominant, unarmed. *Culm leaves* firm, tardily deciduous, the blade erect or reflexed. *Leaf-blades* usually quite long and broad, thick, petiolate with transverse veinlets not at all or only weakly manifest, distant, and oblique. *Inflorescences* of indeterminate branching. *Pseudospikelets* narrowly turbinate, rarely remaining solitary, usually more or less densely aggregated in radiating tufts or heads, the bracts subtending primary pseudospikelets amplexicaul, deciduous. *Spikelets* narrowly conical, terminating in a perfect floret or in a slender prolongation of the rachilla.

Transitional glumes few to several, the lower ones small and slightly indurate, the upper ones increasingly indurate and larger, the uppermost approaching the lemma in size and shape. *Functional florets* solitary, perfect. *Lemma* closely amplectant, strongly indurate. *Palea* closely convolute, thinner and softer in texture than the lemma, dorsally not at all or only obscurely sulcate. *Rachilla* short, disarticulating only below the empty glumes. *Lodicules* 1-several, often conspicuously developed. *Stamens* 6 to ~120, the filaments free, monadelphous, or irregularly connate. *Ovary* solid and rounded, glabrous. *Style* long, columnar, solid below, hollow above, more or less angled, indurate, persistent. *Stigmas* 3-8, verticillate, often wisted together. *Fruit* a long-beaked, ovoid, oblong, or urbinate, non-sulcate caryopsis, the thick pericarp at first fleshy, later indurate.

DISTRIBUTION.—A genus of fewer than 10 species, endemic to southern India and Sri Lanka.

12. *Ochlandra stridula* Moon ex Thwaites

Ochlandra stridula Moon ex Thwaites, 1864:376 [type: Sri Lanka, *C.P. 241*, lectotype, PDA].—Gamble, 1896:123–124, pl. 109.—Gamble in Hooker, 1896:419.—Hooker f. in Trimen, 1900:318–319.—Camus, 1913:181–182, pl. 99: fig. A.—Senaratna, 1956:24.

Bambusa stridula Moon, 1840:26 [nomen nudum; teste Stafleu and Cowan, 1981:566].

Beesha stridula (Moon ex Thwaites) Munro, 1868:145.—Beddome, 1873:234.

Teinostachyum? maculatum Trimen, 1885:273–274 [type: Sri Lanka, Galbodde Tea Estate, Ambagamua, Dec 1883, *C. J. Ferguson s.n.*, lectotype, PDA].

Ochlandra stridula var. *maculata* Gamble, 18[illegible]24.—Hooker f. in Trimen, 1900:319.—Camus, 1913:182.—Senaratna, 19[illegible]5.

MORPHOLOGY

FIGURES 42–44

Plants of unicespitose habit, the rhizomes pachymorph with a short neck, producing a dense clump with closely placed culms. *Culms* soft, when new light brown-maroon becoming dark green, self-supporting below and slightly arched above, 4-5 m tall, ~1 cm in diameter, consisting of ~16 nodes, branching occurring simultaneously from the 7th and above nodes, the lower nodes (except the first two) each with a prophyllate bud which remains dormant; the internodes cylindrical, hollow, those of the mid-culm 39–42 cm long, glabrous except in young culms in which the upper part is covered sparsely with appressed translucent trichomes producing a whitish appearance and roughened surface. *Culm leaves* laminiferous, abscissile upon branching, when new greenish brown below becoming orange-brown to maroon at summit, he blade strongly reflexed and appressed to the sheath, inear-lanceolate, 7.5 cm long, 1 cm wide, with a lateral extension ~2.5 mm long from either side about $^1/_3$ below the attentuate apex, upper surface green, glabrous except for the whitish short-hirsute base and summit, lower surface maroon, glabrous; the sheath with auricles on either side of insertion of the blade bearing antrorsely barbed oral setae 7.5 mm long, the ligule a membrane 1 mm long with an entire margin. *Branch buds* at culm nodes solitary, each containing 3 primordia, a basal dominant one and 2 lateral ones inserted at successive nodes. *Branch complement* at mid-culm nodes unrestricted monoclade, consisting of one strong, central axis and 3 slightly smaller ones on either side, of each set of 3 the central dominant (inserted at proximal basal nodes of the central axis) and the 2 lateral axes (in each group of 3) arising from proximal basal nodes of each of the central lateral axes; each axis consists of 8–12 short basal internodes, each node bearing a sheath and the upper 2 bearing each in addition, a prophyllate bud. *Leafy twigs* 55–81 cm long containing 8–14 leaves; blades lanceolate, tapering to an acuminate apex, the most fully developed 23–34 cm long, 2.5–5 cm wide, glabrous, transverse veinlets not manifest; leaf blades maroon at the base with a thick petiole ~4 mm long, at length abscissile at the level of insertion of the petiole on the sheath; inner ligule a hard, stramineous rim 1.3–2.2 mm long with a ciliolate margin; outer ligule alike but shorter; auricles with oral setae ~7.5 mm long; leaf sheath thick, hard, stramineous, glabrous. *Inflorescence* developing by way of pseudospikelets, forming aggregations terminal to leafy axes, all branches at successive nodes of the main culm flowering or occasional single leafy branches flowering. *Spikelets* ovate-lanceolate, ~3 cm long, 5 mm wide, comprising 3 transitional glumes, 1 lemma, 1 palea, 7 lodicules, 27 stamens, and 1 pistil; transitional glumes firm, ovate, 10–15 mm long with a mucro 2–2.5 mm long, many-nerved (as many as 33 nerves), glabrous except for a few appressed hairs on the upper third, the margins overlapping, ciliate along the overtopping edge; lemma membranous, about as long as the palea with the margins overlapping above, glabrous, 18-nerved with a slight sulcus in the middle, without transverse veinlets; lodicules 7, in 2 alternating whorls, membranous throughout, lanceolate, 3–5-nerved, 10–12 mm long, 1.9–2.5 mm wide; stamens 27, yellow (brown with green tips when mature), with 1 or 2 spicules at the apex of the connective, the filaments filiform, free, basifixed, the anthers opening by an apical pore; ovary glabrous, rounded at the base becoming quadrangular above, with a glabrous quadrangular perigynium enclosing a style, the whorl fused at the base and apex but free for the greater part of the length, the perigynium with a prominent nerve on each corner, dividing terminally into 3 stigmas (one of which divides at its base to produce a fourth); rudimentary rachilla less than 1 mm long present at the base of the sulcus of the palea. *Fruit* not seen.

DISTRIBUTION.—Endemic to Sri Lanka.

ADDITIONAL SRI LANKA SPECIMENS EXAMINED.—COLOMBO DISTRICT: Labugama, *N. Balakrishnan 207* (PDA, US). KEGALLE DISTRICT: Ruwanwelle [Ruanwelle], Nov 1883, *Ferguson s.n.* (PDA; Arandara, Near Galigamuwa, *Soderstrom & Kulatunge 1673* (PDA, US); road to Maliboda from Deraniyagala through Kosgahakanda, *Soderstrom & Kulatunge 1674* (PDA, US); Meenawata, between Deraniyagala and Kosgahakanda, *Soderstrom & Kulatunge 1676* (US); near Arandara, road to Udugama, 7 mi. [11 km] from Kegalle, 4 mi. [6 km] from Galigamuwa *Soderstrom 2563* (B, CANB, DD, K, LE, P, PRE, TNS, US). KANDY DISTRICT: Peradeniya, Royal Botanic Garden, cultivated, *Soderstrom & Kulatunge 1601* (PDA, US). RATNAPURA DISTRICT: Ratnapura [Ratnapoora], Mar 1868(?), *s. coll.*, *C. P. 241* (US fragment ex K, sheet number 2876345). NUWARA ELIYA DISTRICT: Galbode [Galbodde], Ambagamuwa, Dec 1883, *s. coll.* (PDA). GALLE

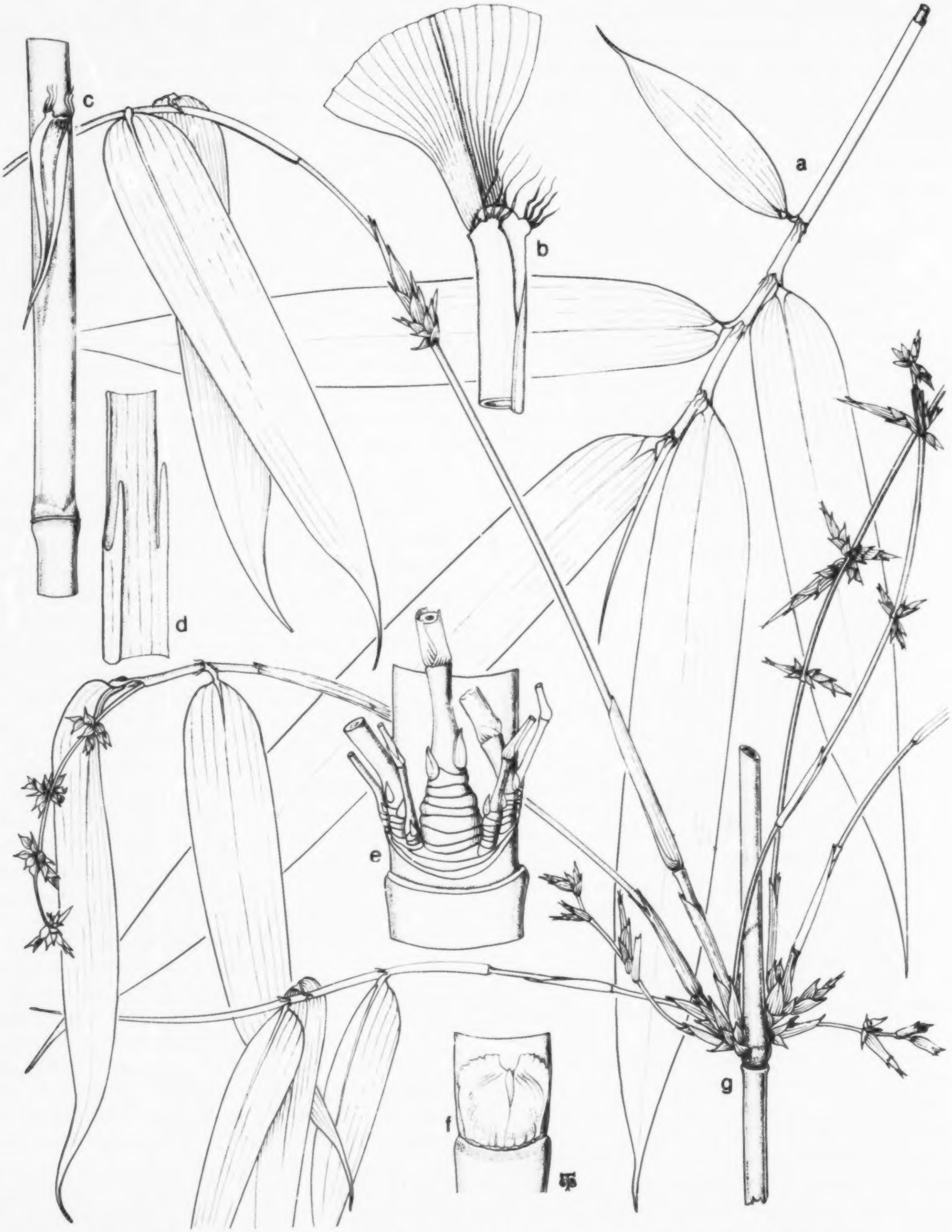

FIGURE 42.—*Ochlandra stridula: a*, leaf complement (×0.6); *b*, leaf ligule (×3.5); *c*, culm sheath in place (×0.6); *d*, upper part of sheath and lower part of blade showing lateral projections (×3.5); *e*, branch complement (×3); *f*, young culm bud (×1.2); *g*, flowering branches (×0.6). (Based on *Soderstrom & Kulatunge 1601.*)

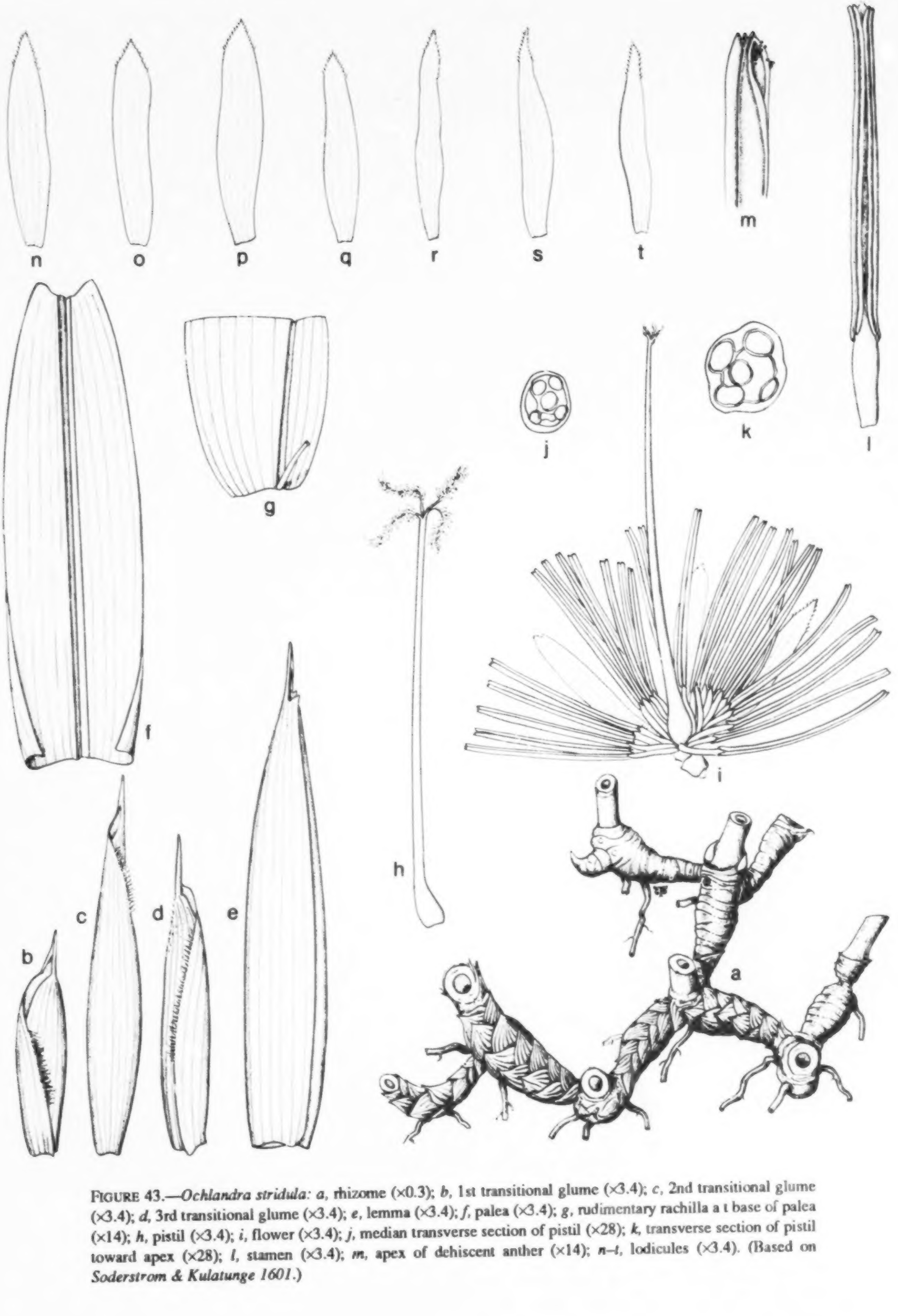

FIGURE 43.—*Ochlandra stridula: a,* rhizome (×0.3); *b,* 1st transitional glume (×3.4); *c,* 2nd transitional glume (×3.4); *d,* 3rd transitional glume (×3.4); *e,* lemma (×3.4); *f,* palea (×3.4); *g,* rudimentary rachilla a t base of palea (×14); *h,* pistil (×3.4); *i,* flower (×3.4); *j,* median transverse section of pistil (×28); *k,* transverse section of pistil toward apex (×28); *l,* stamen (×3.4); *m,* apex of dehiscent anther (×14); *n–t,* lodicules (×3.4). (Based on *Soderstrom & Kulatunge 1601.*)

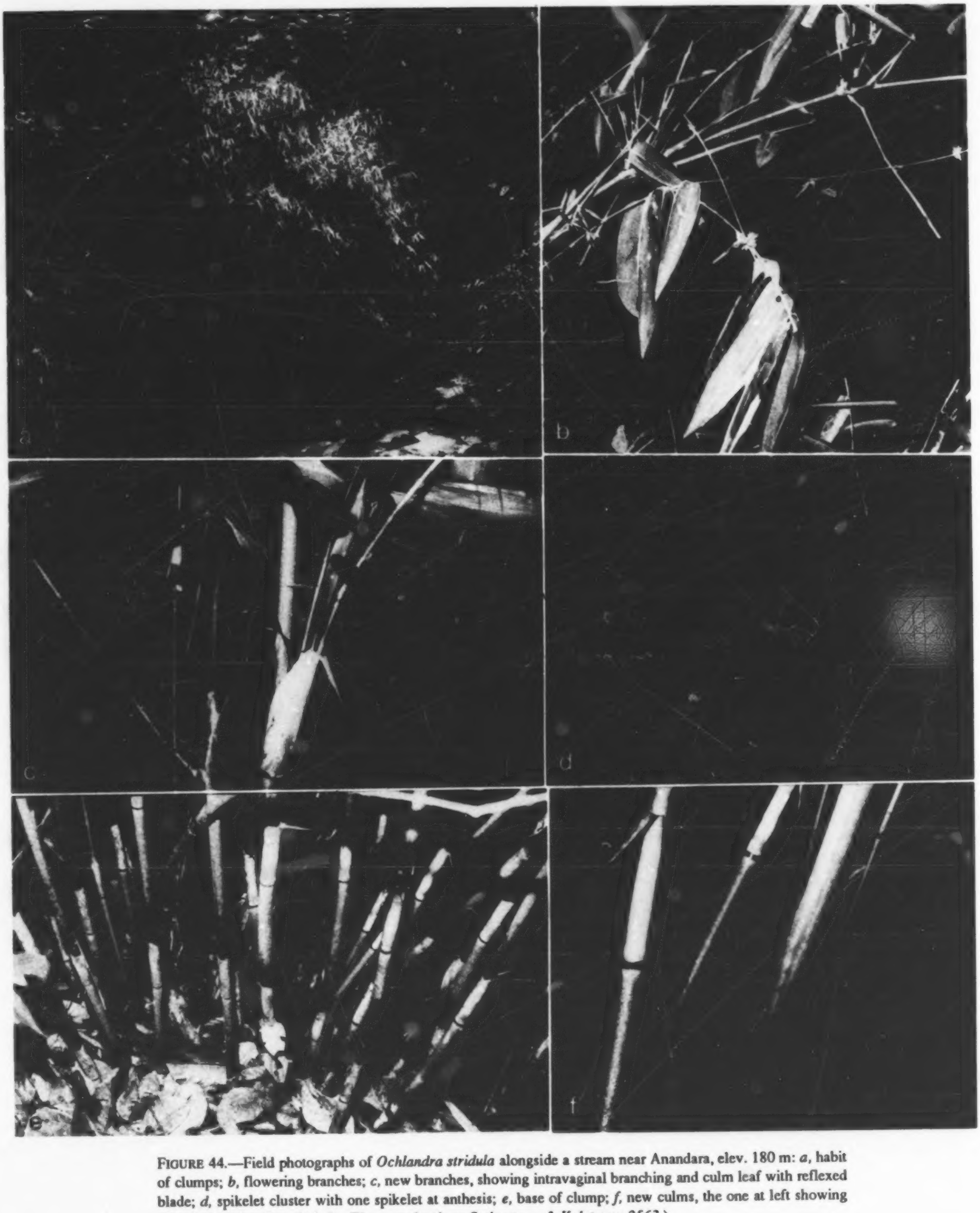

FIGURE 44.—Field photographs of *Ochlandra stridula* alongside a stream near Anandara, elev. 180 m: *a*, habit of clumps; *b*, flowering branches; *c*, new branches, showing intravaginal branching and culm leaf with reflexed blade; *d*, spikelet cluster with one spikelet at anthesis; *e*, base of clump; *f*, new culms, the one at left showing culm leaf with reflexed blade. (Photographs show *Soderstrom & Kulatunge 2563*.)

DISTRICT: Ascent to Haycock Mtn., just W of Hiniduma, *Davidse 7836* (PDA, US). MATARA DISTRICT: ~20 miles [32 km] NE of Galle, S of Hulandawa, *Gould 13424* (PDA, US); Walakanda [Walankande], Sabaragamuwa [Prov.], *Trimen 32* (PDA, US); Walakanda [Walankande], Sabaragamuwa [Prov.], Dec 1893, *s. coll.* (PDA). DISTRICT UNKNOWN: Pitakanda, way to Polwatta, 7 Feb 1929, *de Silva s.n.* (PDA). LOCALITY UNKNOWN: *s. coll., C. P. 241* (US ex W, sheet number 1126305); "Ceylon," *s. coll.* (US, sheets numbered 1021737 and 1021738); *s. coll., C. P. 241, O. C. 1044* (PDA).

DISCUSSION.—We have chosen as lectotype one of two sheets at PDA marked *C.P. 241*. The sheet contains leafy branches with inflorescences and two envelopes. In one envelope are fruits and bracts and in the other are two smaller envelopes containing mounted, beautifully prepared spikelet dissections, which may have been used by Thwaites in writing the original description of the genus. On the sheet itself there appears at the upper right-hand corner in pencil "C.P 241" and "O.C. 1044." On the lower left in ink are the annotations "Beesha ___, Munro" and "Ochlandra stridula, Thw (Enum)," and in pencil "B. verticillata," and "Bambusa stridula Moon Cat." plus an illegible word. Two localities are also penciled on the sheet: Ratnapoora, Mar (?) 18[4]6, and Gardner [illegible] 1853.

A form of the species with purplish mottled culms was first given the name var. *maculatum* by Trimen, who assigned it, questionably, to *Teinostachyum*, in 1885. A few years later he listed the species under *Ochlandra* in the following unpublished list: "1888. Hortus zeylanicus, a classified list of the plants...growing in the Royal Botanic Gardens, Peradeniya, Ceylon."

As lectotype of the name *Teinostachyum? maculatum* Trimen, we have chosen one of several sheets at PDA with a clearly maculate culm. The specimen was collected at Galbodde Tea Estate, Ambagamwa, in December 1883 by Mr. C.J. Ferguson.

The tightly amplectant, indurate lemma of the terminal perfect floret, and the long, columnar, indurate, persistent style with short, verticillate stigmas, relates *Ochlandra* to *Schizostachyum*, which differs most obviously in the non-capitate inflorescence, the tubular nature of the sulcus of the palea in the terminal perfect floret, the less variable, generally smaller number of lodicules, stamens and stigmas, and the much thinner, not fleshy, pericarp of the fruit. McClure (1967) has also noted a possible relationship with *Melocanna* Trinius.

ANATOMY

FIGURE 45

DESCRIPTION.—*Leaf blade in transverse section. Leaf outline:* blade expanded, open; asymmetrical about the midrib (Figure 45*b*); one margin tapering to a definite point, whereas the other is strongly ribbed and not pointed; leaf thickness ~110 µm. *Ribs and furrows:* adaxial surface with slight, rounded ribs and wide, shallow furrows between all vascular bundles (Figure 45*a*); the ribs more pronounced to one side of the midrib (Figure 45*b*) and on the lateral parts of the lamina on the same side; abaxial surface slightly ribbed, with the ribs located opposite the bulliform groups and the furrows corresponding to the costal zones (Figure 45*a*). *Midrib:* abaxially projecting, broadly S-shaped and asymmetrical (Figure 45*b*); vasculature complex with abaxially and adaxially located bundles all embedded in sclerenchymatous, lignified sterome tissue. *Vascular bundle arrangement:* 15 first order bundles present in half the lamina and presumably 29 in complete section; no second order bundles; 5 third order bundles present between successive first order bundles. All bundles located slightly towards the lower side of the leaf. *Vascular bundle description:* third order bundles elliptical, first order bundles round (Figure 45*c*); metaxylem vessels wide, unthickened and elliptical in shape; phloem adjoins the inner bundle sheath. *Vascular bundle sheaths:* inner and outer sheaths present around all vascular bundles (Figure 45*c*); outer sheath entire around the third order bundles but first order bundles with wide abaxial interruptions; no bundle sheath extensions; outer sheath cells numerous with ~16 around third order bundles and ~19 around the first order bundles; these cells rounded and inflated, slightly larger in size around the third order bundles; walls unthickened and lacking chloroplasts (Figure 45*c*). Inner sheath complete, of two layers of uniformly thickened, lignified cells. *Sclerenchyma:* adaxial girders narrow, usually uniseriate, and deep; abaxial girders very wide but short, particularly in association with the first order bundles (Figure 45*c*); no sclerenchyma between the bundles. *Chlorenchyma:* non-radiate, of arm and fusoid cells. Fusoid cavities elongated, downward projecting and present on either side of all vascular bundles in the lower half of the blade thickness (Figure 45*c*); adjacent fusoids separated by 1 or 2 arm cells. Arm cells with very distinct invaginations, particularly the vertically oriented invaginations of the adaxially located arm cells (Figure 45*c*); three layers of arm cells above the fusoid cavities and one below, these with less well-developed invaginations. *Colorless cells:* absent. *Adaxial epidermis:* bulliform cell groups conspicuous, in fans penetrating halfway through the leaf (Figure 45*c*); normally 5 cells are seen to comprise each group as seen in transection; the central cell is not considerably larger than the lateral ones. Outer walls of epidermal cells covered by thick, continuous cuticle; this cuticle much thinner overlying the bulliform cells. No epidermal appendages present. *Abaxial epidermis:* no bulliform cells; costal and intercostal cells similar in transection; epidermal cells covered by a thick, continuous cuticle which is not projected into papillae in the area of the section illustrated (Figure 45*c*); epidermal flanges overlapping the stomata evident; no prickle bases or macrohairs visible.

Abaxial epidermis. Epidermal zonation: costal and intercostal zones differentiated (Figure 45*d*). *Intercostal long cells:*

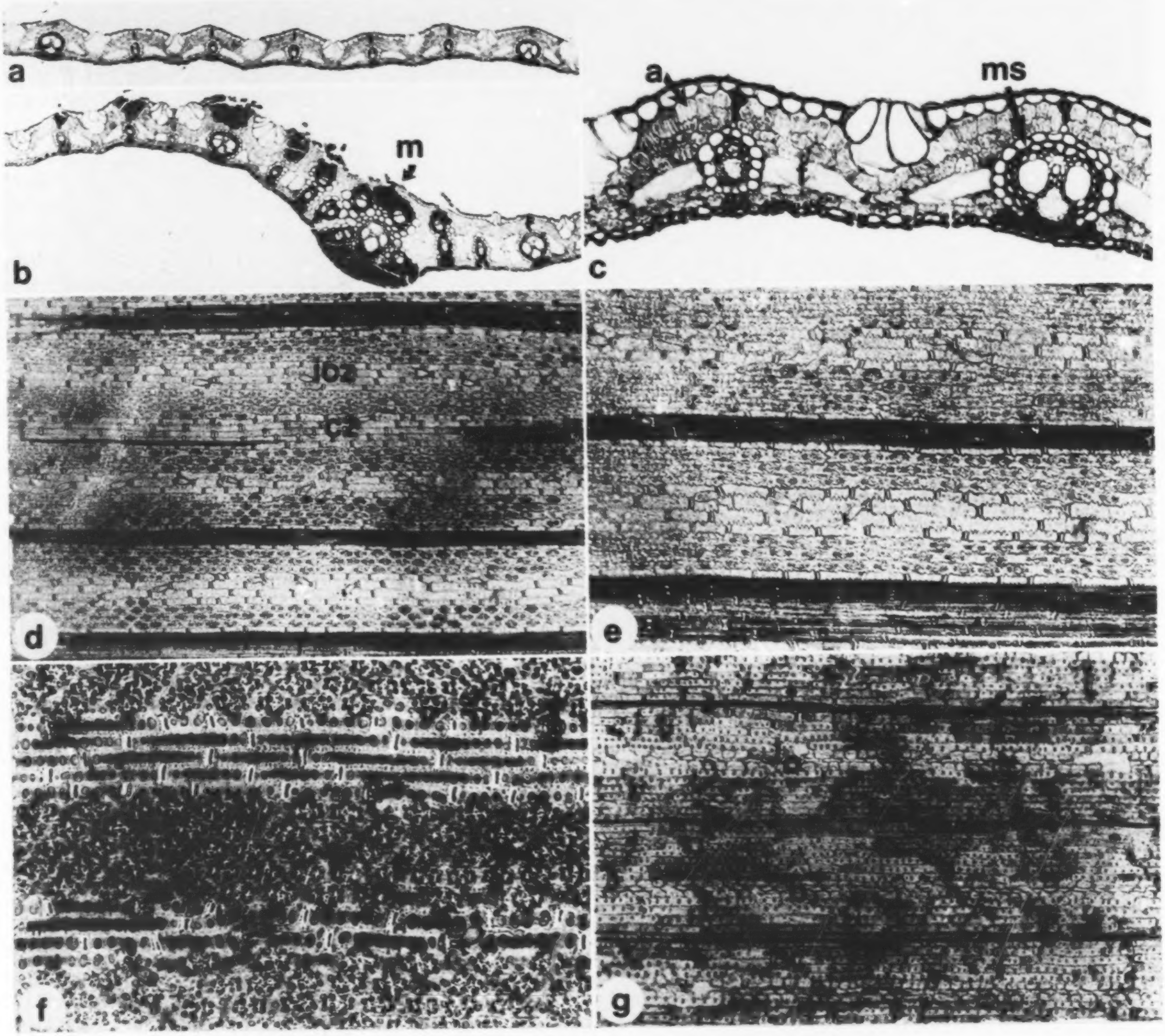

FIGURE 45.—Leaf anatomy of *Ochlandra stridula: a*, outline of midlamina showing arrangement of five third order vascular bundles between successive first order bundles (×58); *b*, midrib (m) with complex vasculature and asymmetrical shape (×58); *c*, detail of blade anatomy showing nature of arm cell invaginations (a), fusoid cavity (f), and multiple layered inner mestome sheath (ms) (×230); *d*, abaxial epidermis showing alternating costal (cz) and intercostal (icz) zones (×93); *e*, abaxial epidermal detail showing tall and narrow silica bodies, microhairs with flask-shaped basal cells, very small papillae on central intercostal files and flanges overarching the stomata (×230); *f*, papillate part of abaxial epidermis illustrating the form and distribution of the cuticular papillae, the flask-shaped microhairs and the tall, narrow silica bodies (×230); *g*, adaxial epidermis with bulliform cells (b), and small refractive papillae on the long cells (×93). (Based on *Soderstrom 2563*.)

elongate-rectangular with parallel, sinuous, unthickened side walls and vertical end walls (Figure 45*d*); cell shape varies across intercostal zones, the central cells being wider and longer. Short cell pairs separate the central long cells and stomata the lateral ones (Figure 45*e*). *Stomata:* shape obscured by overarching flanges (Figure 45*e*) or papillae (Figure 45*f*); 3 or 4 stomatal files on either side of each costal zone; files adjoin one another and one intercostal long cell separates successive stomata in a file. *Intercostal short cells:* paired; both cork and silica cells tall and narrow; present on either side of all long cells in central files of intercostal zones. *Papillae:* variable; either absent or very indistinct (Figure 45*e*) or thickened, cuticular on both costal and intercostal long cells (Figure 45*f*); when absent stomata flanged but when present overlapped by 7 or 8 papillae; both conditions occur on the same leaf blade; papillae with expanded apices arranged in a single row of up to 10 papillae per cell on the costal long cells and the central intercostal long cells (Figure 45*f*); this arrangement not so regular on stomatal intercostal files. *Prickles and hooks:* none observed on specimen studied. *Microhairs:* common; long, more than 4× the stomatal length; distal cell thin walled and narrow but basal cell flask-shaped with thicker walls and cytoplasmic contents (Figure 45*e,f*); located on the central files of the intercostal zones and on the sides of the costal zones. *Macrohairs:* absent. *Silica bodies:* very tall and narrow on intercostal and costal long cells; intimately associated with tall and narrow cork cell; these cork-silica cell pairs alternate with long cells. *Costal cells:* long and short cells identical to intercostal epidermal cells; costal zones narrow, either 3 or 5 cells wide.

Adaxial epidermis (Figure 45*g*). *Intercostal long cells:* elongated, rectangular with slightly sinuous walls; central three files of shorter cells comprise the bulliform cells, interlocking with central file. *Stomata:* very rare and irregular in occurrence; overarched by epidermal flanges. *Intercostal short cells:* tall, narrow silica cells present between most long cells. *Papillae:* cuticular papillae absent; single row of small, refractive papillae present on all long cells; these micropapillae appear to be silicified. *Prickles and hooks:* absent. *Microhairs:* common; similar in structure to those of the abaxial surface although the basal cell is not so inflated. *Macrohairs:* absent. *Silica bodies:* tall and narrow; irregular in occurrence. *Costal zones:* distinguishable only due to underlying fibers; cells structurally identical to those of intercostal zones.

SPECIMEN EXAMINED.—*Soderstrom 2563*, Sri Lanka.

DISCUSSION.—The S-shaped, asymmetrical keel with complex vasculature embedded in sterome tissue is typical of the Schizostachydinae and the Bambusinae. The chlorenchyma consisting of typical arm and fusoid cells, the double-layered inner bundle sheath of uniformly thickened cells, and the fan-shaped bulliform cell groups are other anatomical characteristics shared by these two subtribes of woody bamboos. Transectional leaf blade anatomy, therefore, does not provide evidence for the separation of these subtribes and *Ochlandra stridula* typically has this type of leaf anatomy. Epidermally, however, the presence of large microhairs with unusual thick-walled, flask-shaped basal cells, the presence of small, refractive, adaxial micropapillae on the intercostal long cells, and the absence of epidermal prickles on the epidermides all indicate the the schizostachyoid affinities of *O. stridula.*

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